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THE DIET, DISTRIBUTION, AND PARASITES OF THE BROOK STICKLEBACK,
Calaea inconstans (Kirtland) IN ASTOTIN LAKE, ALBERTA

by



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A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled The Diet, Distribution, and Parasites of the Brook Stickleback, Culaea inconstans in Astotin Lake, Alberta submitted by Michael Christopher Robinson in partial fulfilment of the requirements for the degree of Master of Science.

"Some of the most important discoveries have been made by asking what seem to be very simple questions-- questions so simple, in fact, that they often appear to be stupid. Here is one: What do fish feed on?"

Arthur C. Clarke, 1960.

The Challenge of the Sea.

ABSTRACT

The diet of the brook stickleback in Astotin Lake, Alberta was analyzed over a six-month period in terms of differences in diet associated with time of year, sex, size, horizontal and vertical distribution, and state of health of the fish. Fish infected by Schistocephalus solidus (Muller, 1776) were generally found near the surface, whereas uninfected fish were found near the bottom. Quantitative data were obtained to support the hypothesis that this distributional difference was attributable to a buoyancy change caused by the presence of the parasite. A record of the physical and chemical changes in the lake was kept, invertebrates were collected and identified, and additional information on parasites, variability in spine type, and length frequencies was recorded.

The main objectives of the study were to produce a detailed, comprehensive analysis of the diet of the brook stickleback, and to investigate the significance and possible causes of the peculiar vertical distribution associated with infection by S. solidus. Unlike previous diet studies, this one incorporates large numbers of fish (16 groups of 50). Almost all previous studies of S. solidus have dealt with infections in the threespine stickleback, Gasterosteus aculeatus Linnaeus.

All available aquatic invertebrates were eaten by the fish except adult mites, adult gastropods, and adult dytiscids. Chironomid larvae, cyclopoid nauplii, amphipods, and ostracods were consistently the most important diet items throughout the study period. Differences in diet from month to month were attributable to differences in the relative availability of invertebrate types, as were differences in diet between fish from different parts of the lake. No major differences were found between the diet of males and females. Fish under 35 mm (standard length) generally ate large numbers of the same small organism. Larger individuals tended to eat

a mixture of large and small organisms. These differences were attributable to a difference in mouth size, rather than a distributional difference. The diet of recently - hatched fry consisted primarily of planktonic organisms, possibly a reflection of their limited distribution as well as mouth size. Fish infected with S. solidus ate more planktonic organisms and fewer bottom organisms than uninfected fish, a reflection of their position near the surface. Interesting diet items included sand ingested with non-phryganeid trichopterans, fish eggs, hirudineans, a single case of cannibalism, and an occurrence of gyrodactylid flukes.

Results of the investigation of the peculiar distribution of fish infected by S. solidus was solely responsible. Infected fish had an average P.I. (parasite index) value of 19.37. There was generally one plerocercoid per fish. Dorsal and pelvic spine number was apparently unrelated to susceptibility to infection by S. solidus. There were twice as many females as males among the infected fish examined.

Other parasites included Gyrodactylus eucaliae Ikezaki and Hoffman, 1957, Diplostomum baeri eucaliae Hoffman and Hundley, 1957.

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INTRODUCTION

The brook stickleback, Culaea inconstans (Kirtland), is a North American freshwater representative of the family Gasterosteidae. Most studies concerning this family have dealt with the threespine stickleback, Gasterosteus aculeatus Linnaeus.

Like other gasterosteids, C. inconstans is best known for its reproductive behaviour. Detailed descriptions of its reproduction, both in the field and in the laboratory, are offered by Hall (1956), Winn (1960), McKenzie (1954, 1969a,b), Reisman and Cade (1967), and Smiley (1972).

A number of authors have discussed the tolerance of C. inconstans with respect to alkalinity (Hankinson 1929, Paetz and Nelson 1970), pH (Winn 1960), turbidity (Trautman 1957), salinity (Armitage and Olund 1962), and temperature (Brett 1944). Evermann and Clark (1920), Winn (1960), and Lamsa (1963) have commented on the distribution of C. inconstans in particular bodies of water.

Chen and Reisman (1970) and Nelson (1971) have discussed the phylogeny of C. inconstans. Geographic variation in C. inconstans has been studied by Nelson (1969), and by Nelson and Atton (1971).

The parasites of this fish are listed by Winn (1960) and by Hoffman (1967). Infection by Schistocephalus solidus (Müller 1776) is widely known in G. aculeatus, but not in C. inconstans.

Notes on the diet of C. inconstans are given by various authors. Most of their conclusions are based on evidence from small numbers of fish. For example, Hlavec (1971) based his analysis of seasonal variation in diet on the stomach contents of 20 fish.

The purpose of the present study is to contribute to the existing knowledge of the life history of C. inconstans, with particular regard

to its parasites, distribution, and diet. Since a knowledge of the diet of an organism is essential to the understanding of many other aspects of its biology, the central aim in this study is to present a comprehensive picture of seasonal variation in diet, and to show any differences in diet associated with such factors as sex and size.

Invertebrate collections were made to facilitate the identification of stomach contents by providing easily identifiable reference material. An attempt was made to obtain a reliable quantitative estimate of the relative abundance of invertebrate types, but the numbers of organisms obtained were too small to be statistically useful.

In Astotin Lake, fish infected with S. solidus were often found near the surface. These fish were sluggish, swam with apparent difficulty, and seemed to exhibit curiosity rather than fear. They were lighter in colour than uninfected fish, their distended sides giving them the appearance of tiny white submarines. Infected fish placed in aquaria consistently stayed near the surface, whereas uninfected fish went to the bottom. The significance of this phenomenon was investigated through a comparison of the diets of infected and uninfected fish. Quantitative data were obtained to test the hypothesis that a difference in density was responsible for the difference in vertical distribution. It seemed possible that if the parasite were less dense than the fish, then the overall density of the fish would be reduced by the presence of the parasite within its body. A lower density would result in the infected fish becoming more positively buoyant, barring a reduction in air bladder size (Alexander 1967). The possibility that the difference in behaviour might be caused by an associated infection by another parasite, Diplostomum baeri eucaliae Hoffman and Hundley, 1957 was also investigated.

A careful search for Gyrodactylus eucaliae Ikezaki and Hoffman, 1957

was initiated by the discovery of these flukes as stomach contents of one fish.

LITERATURE REVIEW

The relative hardiness of C. inconstans has been a source of interest to a number of authors. Like Pimephales promelas Rafinesque, with which it is often associated, it has a high tolerance to alkaline conditions (Hankinson 1929, Paetz and Nelson 1970). It is tolerant to a wide range of pH (Winn 1960), but intolerant to turbidity (Trautman 1957).

C. inconstans is the least tolerant of the Gasterosteidae with regard to salinity, but more tolerant than P. promelas and other minnows (Armitage and Olund 1962, Nelson 1968). It could be considered a cold-adapted fish since its upper lethal temperature is relatively low (Brett 1944).

High temperatures have been shown to inhibit breeding in C. inconstans (Winn 1960).

The basic pattern of reproduction in C. inconstans is agreed upon by most authors (Reisman and Cade 1967). The male builds a nest from bits of vegetation which it cements together with kidney secretions. The female is courted and encouraged to lay eggs in the nest. The eggs are subsequently fertilized and cared for by the darker and highly territorial male. The male herds and guards the fry for several days after hatching (Winn 1960). McKenzie (1964, 1969a,b) has categorized and sequentially analyzed the various postures and actions of the male during courtship. Smith (1970) found that adequately-fed fish were more aggressive and territorial than starved fish. Smiley (1972) obtained quantitative data on reproduction from field observations. Most studies on reproduction in this fish, however, have been ethologically-oriented and done in the laboratory. Reproduction in C. inconstans has been summarized briefly by Jacobs (1948), Reisman (1961), and Thomas (1962).

The diet of C. inconstans has been noted by many authors, but most of their comments are brief, and most of their assessments are based on evidence from small numbers of fish. Pearse (1918) is an exception. He examined 110 brook sticklebacks from two consecutive years and listed the diet items as follows: fish eggs, dipterous larvae, hemipterous larvae, May-fly larvae, caddis-fly larvae, chironomid pupae, adult Diptera, Hemipterous adults, podurans, unidentified insects, mites, amphipods, Asellus, ostracods, copepods, cladocerans, snails, Shaeriidae, oligochaetes, rotifers, nematodes, algae, plants, silt, and debris. Like Harlan and Speaker (1956), Winn (1960), and Scott (1967), he summarized by stating, "The brook stickleback ate over 41% insects.....and 38.5% entomostracans (crustaceans)."

Pettit (1902) found that C. inconstans ate mosquito eggs, and suggested its possible use as a practical mosquito and malarial control. Churchill and Over (1933) denied any economic importance of these fish. These authors found that brook sticklebacks ate plants, chironomid larvae, and small crustaceans.

With regard to differences in diet associated with size, Evermann and Clark (1920) stated that of two fish captured in late June, the larger had eaten Entomostraca and insect larvae, the smaller, copepods.

There is little available information on seasonal variation in diet. Evermann and Clark (1920) stated that diet items for December captures consisted of amphipods, cyclopoids, cladocerans, insect larvae, and ostracods. Hlavec (1971) based his analysis of seasonal variation on the stomach contents of only 20 fish. Consequently, the present author feels that his conclusions are of little value.

The diet of brook sticklebacks inhabiting small tributaries was described by Cahn (1927) as being "..... largely insect life, over 50% being small non-aquatic insects that fall into the water."

It is some significance that gastropods, water mites, and fish eggs were noted as diet items by Winn (1960). The colour and the age of mites may be important. White (1918) experimented with colour discrimination in C. inconstans, and concluded that these fish can distinguish between red and green and that they form decided associations respecting the colour of the food they habitually eat. Elton (1922) noticed the avoidance of red mites by G. aculeatus, and experimented with possibility of mimicry in mites in terms of the significance of the red colour and the distastefulness of some of the mites to the fish.

Geographic variation in C. inconstans has received some attention. Hansen (1939) examined the variation in dorsal spine and fin ray number in different populations of C. inconstans. He found that the number of dorsal spines varied between two and seven, and that five was the most common number (71-89%), followed usually by six. Lawler (1957) found a lake (Heming Lake, Manitoba) in which fish with six dorsal spines predominated (66%). He noticed that dorsal spine number tended to increase toward the north. Nelson (1969) has done extensive work on geographic variation. He found clinal variation in dorsal and pelvic spine length. These spines become increasingly shorter in a northwest direction from the midwest. He found no marked geographic variation in the number of pectoral rays, gill rakers, scutes, or vertebrae. According to Nelson and Atton (1971), pelvic spines and girdles are partly or completely missing in individuals of many populations of C. inconstans, one of which is the population at Astotin Lake.

The phylogenetic position of C. inconstans has been a subject for speculation. Chen and Reisman (1970) counted chromosomes in the different members of the Gasterosteidae. They concluded that C. inconstans

and Apeltes quadracus (Mitchill) were probably the most primitive, and that C. inconstans may have been most closely related to the progenitor of the family. A monophyletic origin (from the Aulorhynchidae) is suggested by the presence of large submetacentric pairs of complements in all five North American sticklebacks. However, Nelson (1971) found no acceptable basis in the characters he examined for selecting any living species as being either a primitive form or the most closely allied to the Aulorhynchidae. McInerney and Evans (1970) showed that C. inconstans has a similar developmental pattern to G. aculeatus.

Any information on peculiarities in vertical distribution of C. inconstans is pertinent to the present study. Evermann and Clark (1920) mentioned in their survey of Lake Maxinkuckee that sticklebacks were common in relatively deep water (over 4m) during the summer, and seemed to appear closer to shore during the winter and early spring. Winn (1960) stated, "characteristically the brook stickleback migrates into shallow water to spawn in the spring, after which it gradually moves to deeper water or downstream in the summer." Lamsa (1963) spoke of a downstream movement of brook stickleback occurring in the spring.

A difference in vertical distribution and behaviour associated with infection by S. solidus similar to the one found in the present study has been described in G. aculeatus by various authors (Haitlinger and Wolanska 1965, Lester 1971, and Vik 1954). Since they are more sluggish and closer to the surface, parasitized fish are more conspicuous and more vulnerable to predation by birds (Vik 1954). Several explanations have been advanced to account for this, none of which is entirely satisfactory. Lester (1971) suggested that the oxygen requirement is greater for a fish burdened with the parasite, and that it may be seeking more

oxygen at the surface. Walkey and Meakins (1970) attempted to work out the energetics of the host-parasite system involved here, and found that there is a physiological difference between infected and uninfected fish, but did not relate this to the difference in vertical distribution. Dence (1958) described a similar behavioural difference in common shiners, Notropis cornutus Agassiz, infected with Ligula. However, he reported that these fish stayed near the bottom, rather than near the surface as do C. inconstans and G. aculeatus.

S. solidus has been listed as a parasite of C. inconstans by Hoffman (1967), but practically all of the literature on S. solidus deals with infections in G. aculeatus. A complete literature and taxonomic review of S. solidus can be found in Vik (1954) up to that date. Vik (1954) found 100% infections in six out of nine lakes, and the occurrence of only one worm per fish in 56% of the cases he examined. He found as many as 16 worms in one fish. Threlfall (1968) found a population of G. aculeatus in which there was a 99.09% infection, and an average of 3.0 worms per fish. Markley (1940) found an infection of 39%, and an average of 2.29 worms per fish. Haitlinger and Wolanska (1965) found a 62% infection with fish containing only one worm predominating (36%). They noticed a great deal of morphological variability among larvae, suggesting a variety of developmental possibilities. Arne and Owen (1967) have reviewed the pathological effects of S. solidus on G. aculeatus, among which are a disturbance of breeding behaviour, a reduction in liver weight, a delay in oöcyte maturation, and a gross distention of the body causing difficulty in locomotion. Hopkins and Smyth (1951) have summarized the work of others, and add a few experimental results of their own. They attribute the fact that adult S. solidus are rare to a rapid maturation rate in the final host. Orr, Hopkins, and Charles (1969)

have demonstrated the specific nature of S. solidus with regard to its intermediate host.

Two trematodes were involved directly in the present study. Metacercaria of the trematode Diplostomum baeri eucaliae Hoffman and Hundley, 1957, occur in the brain of C. inconstans. The life cycle of this parasite has been discussed by Hoffman and Hundley (1957), and summarized by Hoffman (1960). Localization of the worms in the choroid plexus and optic lobes of the fish's brain has been dealt with by Hoffman and Hoyme (1958). The snail, Stagnicola palustris, and the mallard duck, Anas platyrhynchos, have been named as hosts.

The monogenetic trematode Gyrodactylus eucaliae Ikezaki and Hoffman, 1957 was first discovered on the skin, gills, and fins of C. inconstans. The possibility of an actively acquired immunity by the host has been discussed by Ikezaki and Hoffman (1957). Lester (1971) described the method of attachment of these flukes to Gasterosteus aculeatus Linnaeus and their rejection by a sloughing of mucus every one or two days. Later that year, however, in a personal correspondence to Mr. W. Bethel, he stated that "a similar slough is sometimes regularly produced by fish that have never been infected by the flukes so the response is perhaps more general than appeared at first."

THE STUDY AREA

Astotin Lake (long. 112° 51' west, lat. 53° 41' north) is situated about 37 kilometers east of Edmonton in Elk Island National Park. The lake lies in an area characterized by 'knob and kettle' topography, thought to be the result of Wisconsin glaciation (Kevan 1970).

The lake occupies 5.62 sq. km. and has an average depth of about 3 m. There is one small pocket about 7 m. deep, just northeast of High Island (Fig. 1).

Fig 1. Map of Astotin Lake showing the three study areas (after Lin 1968).



The gently sloping lake bottom consists of silt, mud, sand, and marl deposits (Lin 1968). In many parts of the lake, the bottom is covered by a thick mat of organic debris and algae.

Algal blooms are a common occurrence at Astotin Lake, the important representatives of the phytoplankton being Anabaena spp., Aphaizomenon flos-aquae, and Microcystis aeruginosa (Lin 1968). Higher aquatic plants are also well-represented. During the summer of 1970, in most parts of the lake, there was a strip of rooted submergents about 15m wide along the shore, with its inner edge about 3 m offshore.

Astotin Lake may be considered eutrophic because of its shallowness, high productivity, high summer temperatures, large quantity of organic debris, and periods of low oxygen concentration (Lin 1968).

Before 1932, the lake was drained by Astotin Creek (Fig. 1), which originated at the north end of the lake, followed the northwesterly slope of the surrounding terrain, and emptied into the North Saskatchewan River (Lin 1968). The damming of the creek in 1932 had a great effect on the lake and on its fish fauna. The prevention of drainage probably accelerated the process of eutrophication (Lin 1968). Evidently, northern pike Esox lucius Linneaus and suckers Catostomus sp. were present in the lake in great numbers until the spring of 1932, when hundreds of dead fish were found lying on the shore. The two species were completely eliminated by winterkill in 1933, and reinvasion was prevented by the dam (Lin 1968). Another possible effect can be found in the statement by Nelson and Atton (1971) that "there is a greater tendency for individuals (brook sticklebacks) in which the pelvic skeleton is deficient to occur in lakes which lack an outlet rather than to occur in lakes with a permanent outlet."

For years, the brook stickleback Culaea inconstans (Kirtland), a fish capable of surviving periods of low oxygen, was the only indigenous fish reported from the lake. In 1971, there was a report of fathead minnows, Pimephales promelas Refinesque. This report came after a period of heavy rains and flooding in the area, which probably accounts for their sudden appearance.

In recent years, a high proportion of the stickleback population has been infected with S. solidus plerocercoids. Great numbers of piscivorous waterfowl provide hosts for the adult cestodes (Kevan 1970), while cyclopoid copepods provide hosts for the coracidia (Vik 1954).

MATERIALS AND METHODS

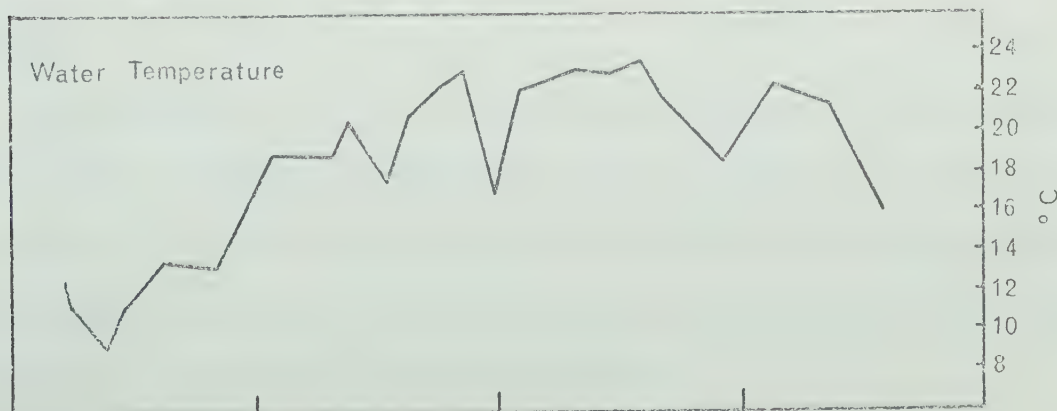
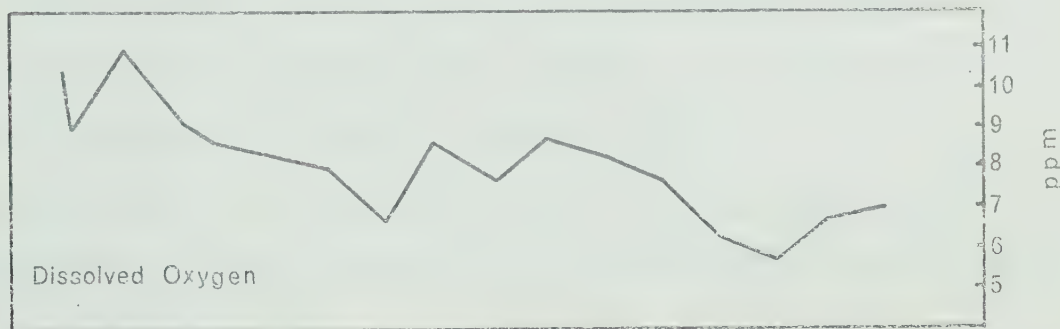
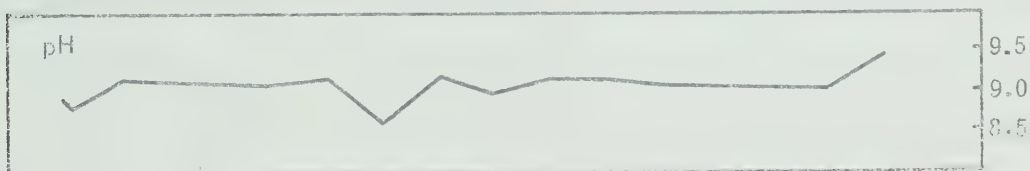
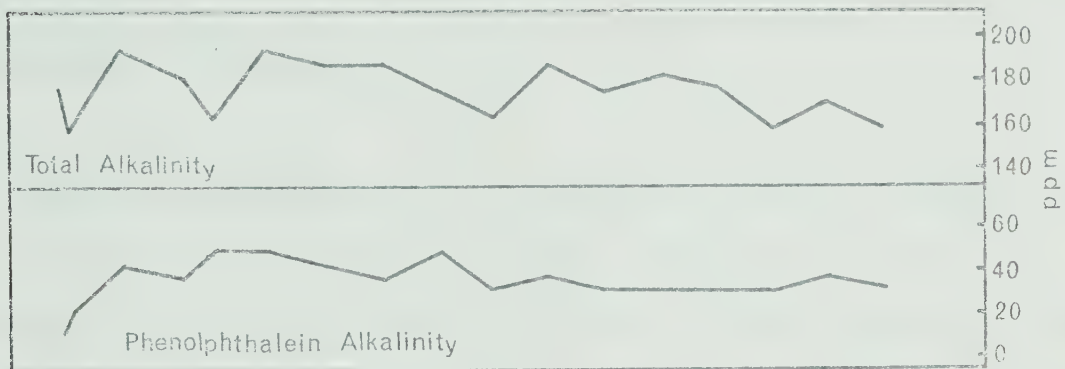
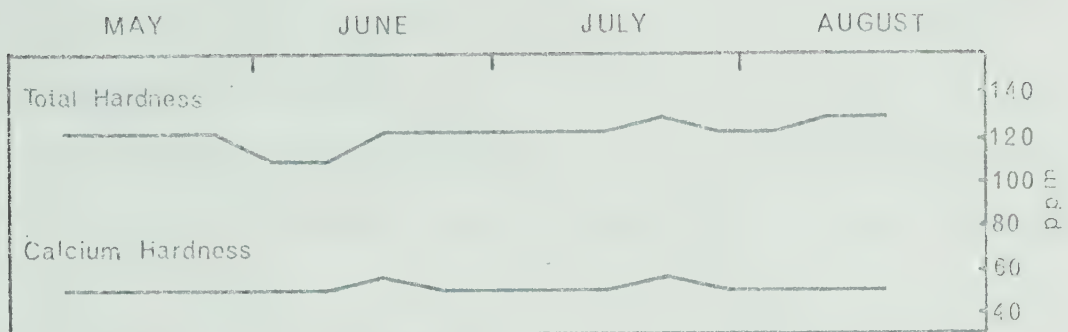
Three study areas (Fig. 1) were chosen on the basis of their accessibility and their suitability for a companion study on reproduction (Smiley 1972). At Residence Point, the water was relatively calm, the bottom consisted of organic ooze and sand, and rooted aquatics were well-established. At High Island, the situation was similar, but there was more exposure to wind and waves. Youth Hostel Bay was most susceptible to the effects of wind and waves. The bottom of the bay consisted largely of gravel and sand, rooted aquatics were not well-established, and algae was inclined to accumulate.

Semi-weekly trips were made to the lake from April 30 to September 1, 1970. Physical and chemical data were recorded at each of the study areas on each of these trips for the purpose of providing background information on the lake. Weekly collections of fish were made using a seine net at each location. Several invertebrate collections were made during the summer of 1970, and an additional invertebrate collection was made on July 11, 1971.

As much biological information as possible was obtained from the fish. Most of the fish were arranged in 16 groups, each group consisting of 50 randomly-selected fish for a particular date and location. The standard length, number of dorsal spines, number of pelvic spines, sex, parasites, and stomach contents were recorded for each fish. Additional studies were carried out to show more clearly the differences in diet between large and small fish, and the differences between fish infected by S. solidus and uninfected fish.

Density calculations were made in an attempt to show that density differences were responsible for the difference in vertical distribution

Fig. 2. Chemical and physical changes in Astotin Lake during the summer of 1970.



between fish infected by S. solidus and uninfected fish.

The examination of large numbers of additional fish provided valuable data on parasites.

Because of the difficulty in estimating the age of fish once they have been fixed in formalin (Jones and Hynes 1950), length frequencies were plotted (Appendix C) to give some indication as to how length might correspond to age classes.

PHYSICAL AND CHEMICAL DATA

METHODS

Semi-weekly measurements of temperature, dissolved oxygen, pH, alkalinity, and hardness were made during the summer of 1970 at the three study area. Water samples were taken from areas normally occupied by fish. Phenolphthalein alkalinity, total alkalinity, calcium hardness, and total hardness were estimated using Hach Kit PO-9A. Hach Kit #OX-10 was used for estimating the amount of dissolved oxygen, Metrohm #E2804 was used for estimating pH, and Tele-thermometer #43 TD was used for taking measurements of temperature. Temperature readings were taken in 1.2 m of water, at the surface immediately above that location, and at the surface near the shore. Readings from the three study areas were averaged for each date, and it is these averages that are plotted on the graphs in Fig. 2.

RESULTS

As can be seen in Fig. 2, fluctuations in hardness, alkalinity and pH were small. Temperature gradually increased during the summer, and then began to decrease with the approach of autumn. The amount of dissolved oxygen gradually decreased during the summer. Oxygen never dropped below 5 ppm, at least not during the daytime.

THE INVERTEBRATE FAUNA

METHODS

At each of the three study areas, bottom samples were taken during the day at depths of 0-30.5 cm, 30.5-61.0 cm, 61.0-91.5 cm, and 91.5-122 cm, using a 15 cm Ekman dredge. These depths cover the depths normally inhabited by fish. Unfiltered sediment from each sample was preserved in a small jar to be analyzed later for micro-invertebrates. The remaining quantities of all samples were pooled and sieved through a #30 screen (poresize 0.59 mm). Invertebrates retained in this process were stored in separate jars for each location. Specimens were fixed in 10% formalin.

Because of the large amount of vegetation in the lake, a Birge cone net was used to collect micro-plankton. The net was dragged by hand (close to the surface) in a direction paralleling the shore for about 15 m at each of the aforementioned depths. Macro-plankton was collected in the same manner, using a bucket with its bottom consisting of #30 screen.

Invertebrates were counted and identified (to the species level, wherever possible). Rhodamine-B was used to facilitate separation of invertebrates from the sediment (Hamilton 1968). Keys, particularly those found in Pennak (1953), Usinger (1968), and Edmondson et al. (1966) were used extensively, and reference collections were used to confirm identification in some groups.

The methods referred to above were used during each of the five 1970 collections. In the 1971 collection, the aim was to provide additional information on the lake, and sampling was done with a view to gathering as many different invertebrates as possible. Seine nets, dip nets, and a 15 cm Ekman dredge were used extensively, but with no intention of quantifying the results.

Table 1. An estimate of the relative abundance of invertebrates present in Astotin Lake during the summer of 1970

Invertebrate Group	Residence Point	High Island	Youth Hostel Bay	Total	% Number
Chironomidae larvae	41	83*	125	249	47.0
Trichoptera larvae	29	22	21	72	13.6
Amphipoda	18*	28	7	53	10.0
Hirudinea	41	3	7	51	9.6
Pelecypoda	15	11	13*	39	7.4
Oligochaeta	1	7*	13	21	4.0
Ostracoda	14	0	0	14	3.4
Gastropoda	2	0	3	5	0.9
Dytiscidae	0	2	1	3	0.6
Ceratopogonidae larvae	1	1	0	2	0.4
Culicidae	0	0	2	2	0.4
Unident. Insecta	0	1	0	1	0.2
Total	175	162	193	530	100.0

* These values were arrived at by averaging the other two. The original values were considered to be inordinately high due to sampling error.

RESULTS

Table 1 represents an approximate estimate of the relative abundance of invertebrate types over the whole summer, and is based on totals obtained from the five collections made at each of the three study areas in 1970. This may be compared with total breakdowns of diet items given in the subsequent section, but cannot be considered complete since many organisms found as stomach contents (particularly micro-plankton) were not found in invertebrate samples (see DISCUSSION).

Of the organisms represented in Table 1, chironomid larvae were by far the most numerous. Trichopteran larvae, amphipods, hirudineans and pelecypods were also extremely abundant. Oligochaetes and corixids were not as numerous, but were consistently present and were usually found in larger numbers than gastropods, adult dytiscids, ceratopogonid larvae, and culicid larvae. Ostracods were apparently more abundant than Table 1 suggests.

The following is a list of the invertebrates found in Astotin Lake during the summer of 1970 based on invertebrate collections and on fish stomach contents:

Phylum MOLLUSCA

Class GASTROPODA

Gyraulus parvusPhysa gyrina

Class PELECYPODA

Pisidium sp.

Phylum ANNELIDA

Class OLIGOCHAETA

Chaetogaster sp. and others

Class HIRUDINEA

Erpobdella punctataGlossiphonia complanataNephelopsis obscuraPlacobdella ornataPlacobdella parasitica

Phylum ARTHROPODA

Class CRUSTACEA

Subclass BRANCHIOPODA

Order DIPLOSTRACA

Suborder CLADOCERA

Acroperus sp.Bosmina longirostrisDaphnia magna

Subclass OSTRACODA

Order PODOCOPA

Candona sp.Cyclocypris amplaCyclocypris ovumCypria sp.Cypridopsis sp.Limnocythere sp.

Subclass COPEPODA

Order CYCLOPOIDA

- unidentified immatures
- probably Cyclops sp.

Subclass MALACOSTRACA

Order AMPHIPODA

Gammarus lacustrisHyalella azteca

Class INSECTA

Order ODONATA

Enallagma sp.

Order HEMIPTERA

Dasycorixa hybrida

Order COLEOPTERA

Acilius sp.Haliplus sp.Hydroporus sp.Oreodytes sp.

Order TRICHOPTERA

Molanna sp.Oecetis sp.PHRYGANEIDAE (probably
Agrypnia sp.)

Order DIPTERA

CERATOPOGONIDAE (Bezzia or
Probezzia sp)CHIRONOMINAE (Tanytarsus sp.
and others)

In the interest of adding to the information on the invertebrates of
Astotin Lake, the following list of invertebrates collected on July 11,
1971 was compiled:

Phylum MOLLUSCA

Class GASTROPODA

Helisoma trivolvisPhysa gyrinaLymnaea stagnalis

Phylum ANNELIDA

Class HIRUDINEA

Erpobdella punctataGlossiphonia complanataPlacobdella ornata

Phylum ARTHROPODA

Class CRUSTACEA

Subclass BRANCHIOPODA

Order DIPLOSTRACA

Suborder CLADOCERA

Daphnia magna

Subclass MALACOSTRACA

Order AMPHIPODA

Gammarus lacustrisHyalella azteca

Class ARACHNIDA

Order ACARINA

Eylais sp.Hydrachna sp.

Class INSECTA

Order ODONATA

Enallagma borealeEnallagma ebrium

Order HEMIPTERA

Dasycorixa hybridaDasycorixa rawsoniGerris dissortisMicrovelia pulchellaNotonecta kirbyi

Order COLEOPTERA

Acilius sp.Graphoderus sp.Ilybius sp.Laccophilus sp.

Order TRICHOPTERA

Oecetis sp.Trianodes sp.

Order DIPTERA

Chironomus sp.

THE DIET OF THE BROOK STICKLEBACK

METHODS:

Since there are many ways of assessing the importance of food organisms, the possibilities were considered before an approach was decided upon. Some of the possible methods are discussed below.

One method is simply to count the different organisms which have been eaten, and to express these counts as a percentage of the total number of organisms. Results expressed in this way can be deceiving, since food organisms are of different sizes. For example, one amphipod might weigh as much, occupy the same volume, or have the same food value as several hundred cladocerans.

Another approach is to weigh the organisms, or to multiply the number of organisms by a calculated average weight for each type of organism. Weight can be expressed as a percentage of the total weight of either the food organisms or the fish. Volume can be dealt with similarly. A time-saving improvement, used by Hynes (1950), is to use a rough estimate of volume by assigning arbitrary numbers of points to food organisms according to how much estimated volume they would occupy in a stomach. A further improvement, suggested by Hynes (1950), is to assign points to stomachs on the basis of their fullness, then subdivide the points among the food organisms present in each stomach.

Another method is to express the number of times that a particular food organism is the dominant stomach content as a percentage of the number of stomachs. This method has the obvious flaw of neglecting organisms which are always present but never dominant.

Frequency of occurrence is another way to assess the importance of food organisms. The number of times a particular organism occurs can be expressed as a percentage of either the total number of stomachs or the total number of occurrences.

For the present study, it was decided that a combination of the above methods was the most satisfactory way to express the importance of food items. Fish stomachs were removed and assigned an arbitrary number of points according to their estimated fullness. Stomach contents were used, since food organisms are generally unrecognizable in other parts of the gut. A full stomach was given 20 points, a half-full stomach 10, and so on. This eliminated the problem of dealing with fish of different sizes, and made it possible to group fish randomly, or in any other conceivable arrangement. For example, a large fish with a full

stomach might have eaten four amphipods of approximately equal size, each of which would be assigned five volume points for a total of 20. A smaller fish with a full stomach might contain one amphipod, which would be assigned 20 points. In this way, the amphipod food category would be fairly assessed in terms of importance to the fish. Actual counts of organisms were made where feasible, but where extremely large numbers of small organisms occurred in a single stomach, approximate counts were made. It was impossible to count such items as detritus and sand. The frequency of occurrence of each item was also calculated as a percentage of the total number of occurrences for each sample.

The stomach contents of 800 fish were examined. The fish were arranged in groups of 50. Eight groups were taken from collections made at Residence Point over a six-month period. Four groups were taken from collections made at High Island corresponding to four dates on which Residence Point collections were made. Similarly, four groups were taken from Youth Hostel Bay collections corresponding to the same dates. For each fish, the following information was recorded: standard length, sex, number of dorsal spines, number of pelvic spines, parasites, fullness of stomach, and the names, numbers, and volume points for all food organisms present. With this experimental design, it became possible to demonstrate seasonal variation in diet, and to demonstrate differences in diet associated with sex, size, spine type, or location in the lake.

The relative importance of diet items is expressed in terms of percentages of numbers, estimated volume, and frequency of occurrence in many of the tables. Complete analyses of each sample are given in Appendix A. It was felt that the single most graphic way of expressing the results was to show frequency of occurrence in the form of a divided circle, in

which 360 is equal to 100%. Hartley (1948) used histograms showing frequency of occurrence for the same purpose.

An additional sample of fry was collected with a dip net on July 3, 1970 at Residence Point. The stomach contents of 79 fish were examined. The stomach contents of 18 of these fish were analyzed in terms of percent number and frequency of occurrence.

RESULTS

A) SEASONAL VARIATION IN DIET

The seasonal changes in diet from April 30 to October 17, 1970 are presented in Fig. 3 and summarized in Table 2. The importance of the main food items can be readily seen.

From Fig. 3 and Table 2, it is apparent that chironomid larvae, cyclopoid nauplii, amphipods, and ostracods were important diet items throughout the study period. Hirudineans, ceratopogonid larvae, and algae appear to have lost importance as the summer progressed, whereas cladocerans, corixids, and water mites seem to have gained significance. Trichopteran larvae, pelecypods and gastropods were apparently restricted as diet items to late summer and early autumn. Culicid eggs preceded culicid larvae as diet items. The occurrence of fish eggs in stomachs corresponds with the breeding period. Detritus did not appear to be restricted by time of year, but sand occurred only in late summer and early autumn. Dytiscid larvae appeared in the diet for only a short time.

The results are totalled in Table 3 and Fig. 4. A complete analysis of each sample is given in Appendix A.

B) A COMPARISON OF DIET AT THE THREE STUDY AREAS

Based on 12 samples, four from each study area and each consisting of 50 randomly-selected fish, a comparison of diet at the three study

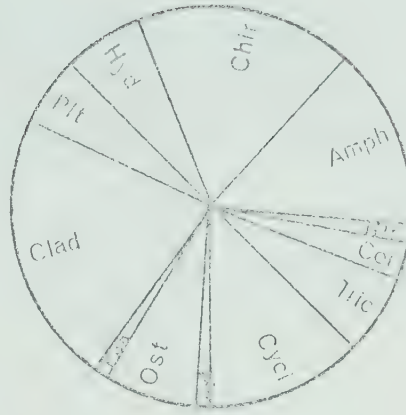
Fig. 3 Seasonal variation in diet based on the stomach contents of 400 fish collected at Residence Point and expressed in terms of frequency of occurrence of diet items. Each circle represents a total analysis of the stomach contents of 50 fish. $360^{\circ} = 100\%$.

Algae	Alg
Amphipoda	Amph
Ceratopogonidae larvae	Chir
Cladocera	Clad
Corixidae	Cor
Culicidae	Cul
Culicidae eggs	C. eggs
Cyclopoida nauplii	Cycl
Detritus	Det
Dytiscidae larvae	Dyt
Fish	Fish
Fish eggs	F. eggs
Gastropoda	Gast
Hirudinea	Hir
Oligochaeta	Olig
Ostracoda	Ost
Pelecypoda	Pel
Sand	Sand
Terrestrial Arachnida	Arac
Trichoptera larvae	Tric
Unident. animal material	Anim
Unident. Insecta	Ins
Unident. plant material	Plt
Unrecognizable material	Unre
Zygoptera numphs	Zyg

APRIL 30



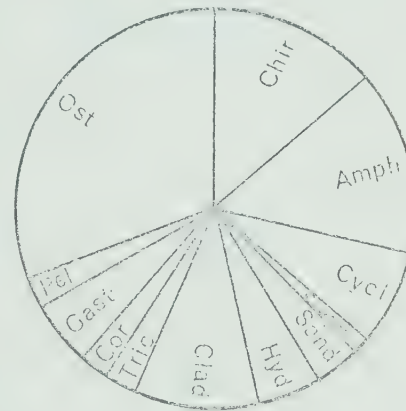
JULY 21



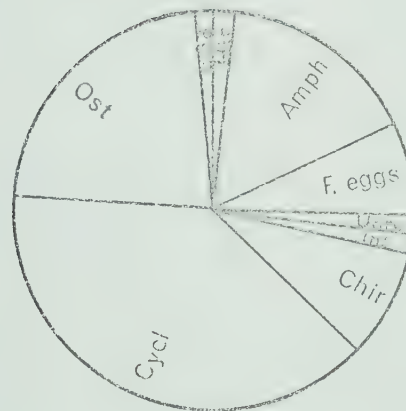
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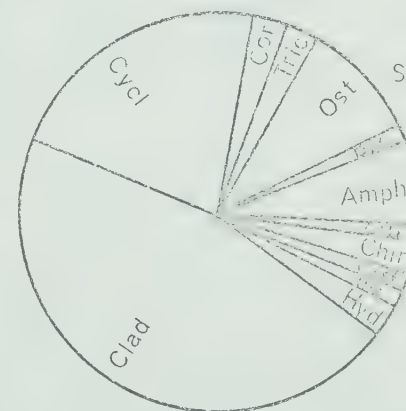
AUGUST 11



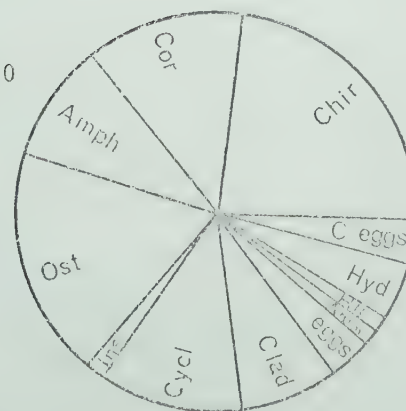
JUNE 9



SEPTEMBER 1



JUNE 30



OCTOBER 17

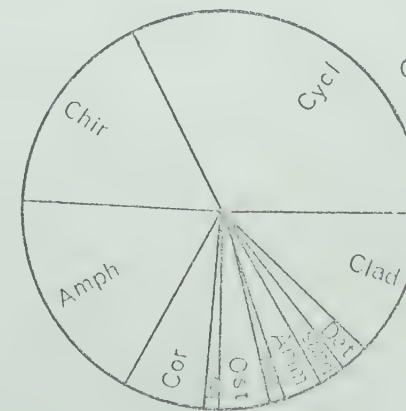


Table 2. The occurrence of food organisms as diet items in fish collected at Residence Point. Fifty fish stomachs were examined for each date. 'Unidentified' and 'Unrecognizable' categories have been omitted since they only reflect difficulty in identifying stomach contents in particular cases.

Diet Item	Apr.30	May 22	Jun.9	Jun.30	Jul.21	Aug.11	Sep.1	Oct.17
Chironomidae								
larvae	X	X	X	X	X	X	X	X
Cyclopoida								
nauplii	X	X	X	X	X	X	X	X
Hirudinea	X		X	X	X			
Ceratopogonidae								
larvae	X							
Algae	X	X						
Ostracoda	X	X	X	X	X	X	X	X
Detritus		X					X	X
Amphipoda		X	X	X	X	X	X	X
Fish eggs		X	X					
Cladocera			X	X	X	X	X	X
Corixidae				X	X	X	X	
Hydracarina				X	X	X	X	
Culicidae eggs				X		X		
Fish					X			
Dytiscidae								
larvae					X			
Trichoptera					X	X	X	
Pelecypoda						X		X
Gastropoda						X	X	
Sand						X		X
Culicidae								
larvae							X	

Table 3. The relative importance of food items over a six-month period based on the stomach contents of 400 fish taken at Residence Point.

Diet Item	% Occurrence	% Number	% Volume Points
Cyclopoida nauplii	9.64	45.36	25.38
Chironomidae larvae	9.64	8.08	20.80
Amphipoda	8.43	3.94	15.53
Cladocera	7.23	22.10	14.20
Ostracoda	9.64	16.36	8.62
Corixidae	6.02	0.65	4.11
Trichoptera larvae	3.61	0.09	1.87
Unident. animal material	3.61	-----	1.74
Hirudinea	4.82	0.09	1.50
Unident. Insecta	7.23	0.11	1.18
Fish eggs	2.41	0.64	0.94
Algae	2.41	-----	0.62
Unrecognizable material	1.20	-----	0.58
Culicidae eggs	2.41	1.46	0.39
Fish	1.20	0.01	0.37
Gastropoda	2.41	0.21	0.37
Hydracarina	4.82	0.42	0.36
Sand	2.41	0.23	0.36
Culicidae	1.20	0.10	0.35
Detritus	3.61	-----	0.29
Pelecypoda	2.41	0.06	0.21
Dytiscidae larvae	1.20	0.01	0.09
Unident. plant material	1.20	-----	0.09
Ceratopogonidae larvae	1.20	0.08	0.06

Fig. 4 The relative importance of diet items over a six-month period based on the stomach contents of 400 fish collected at Residence Point and expressed in terms of frequency of occurrence.

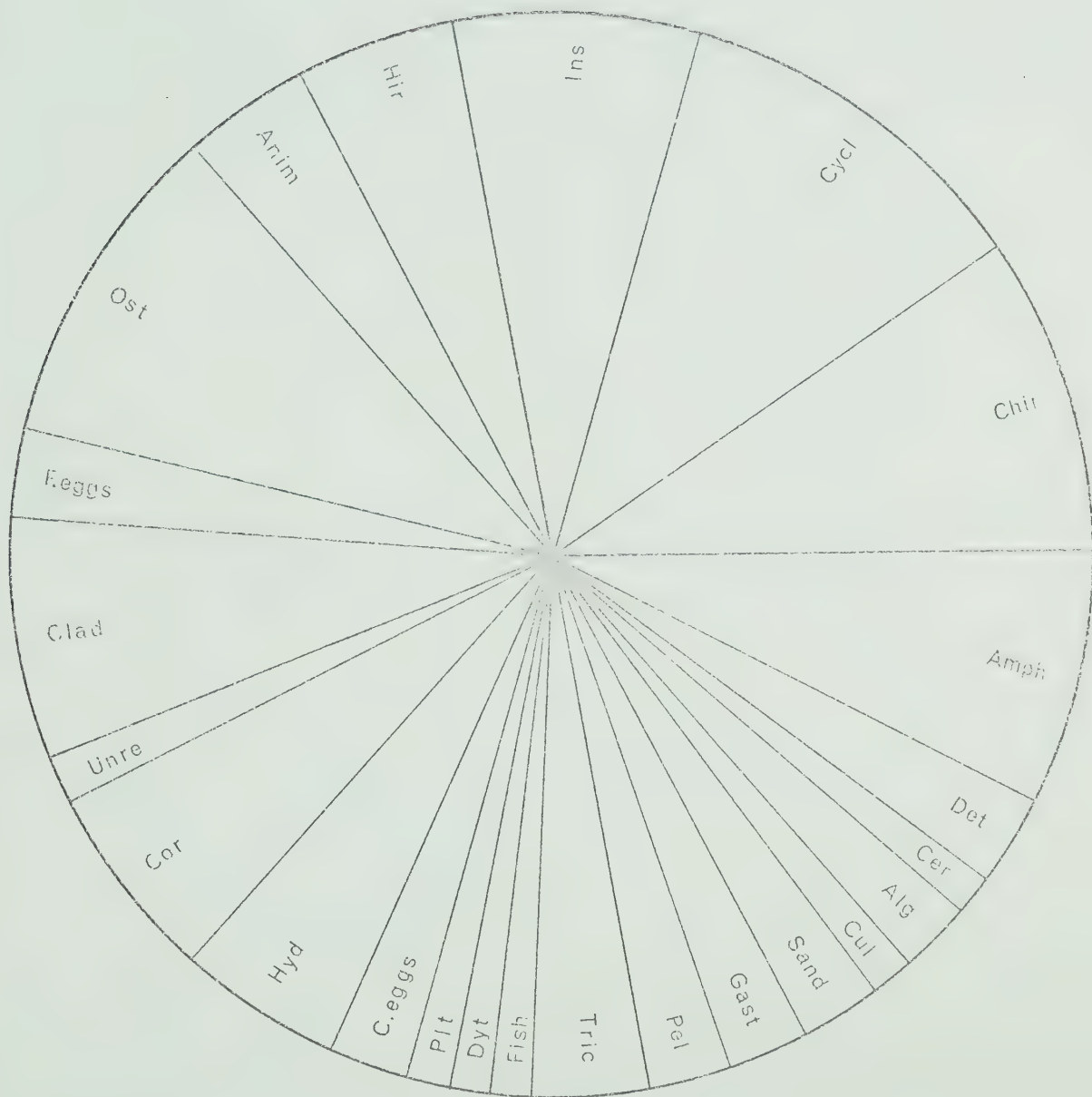
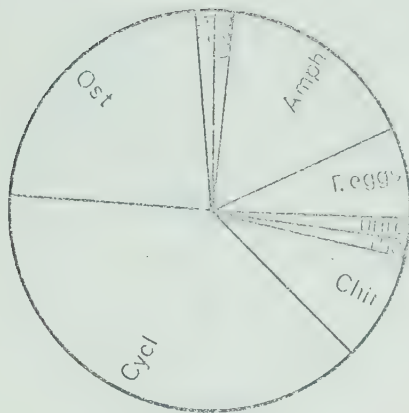
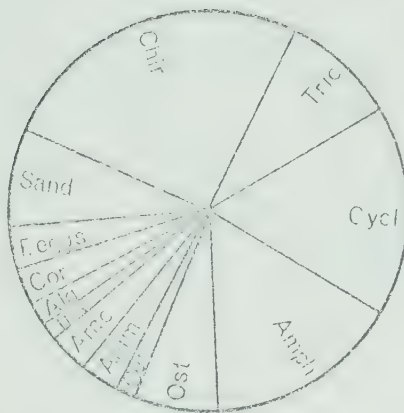


Fig. 5 A comparison of fish diet at the three study areas on four dates based on the stomach contents of 600 fish.

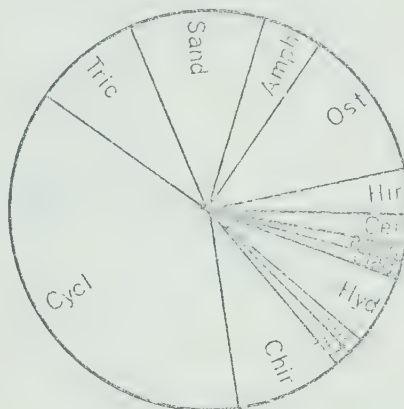


RESIDENCE POINT

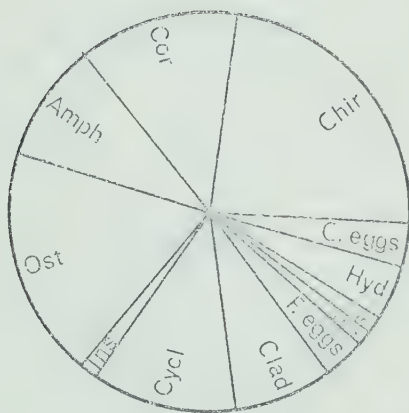


YOUTH HOSTEL BAY

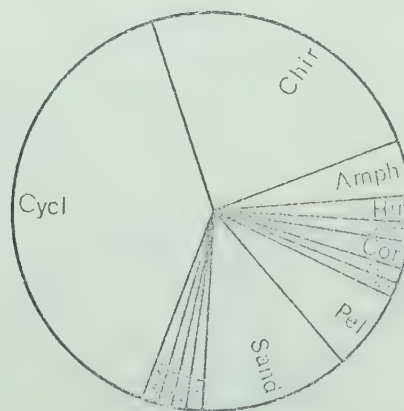
JUNE 9.

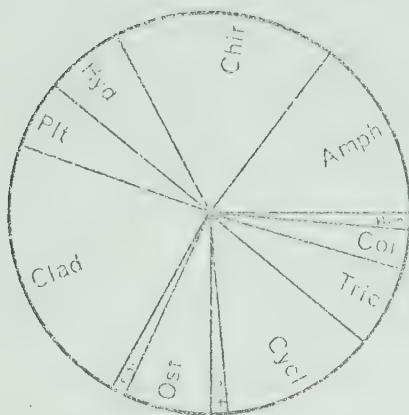


HIGH ISLAND



JUNE 30.



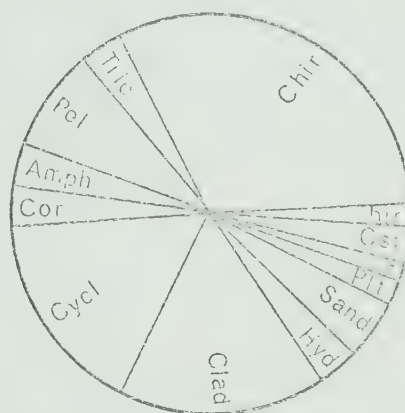


RESIDENCE POINT



YOUTH HOSTEL BAY

JULY 21.



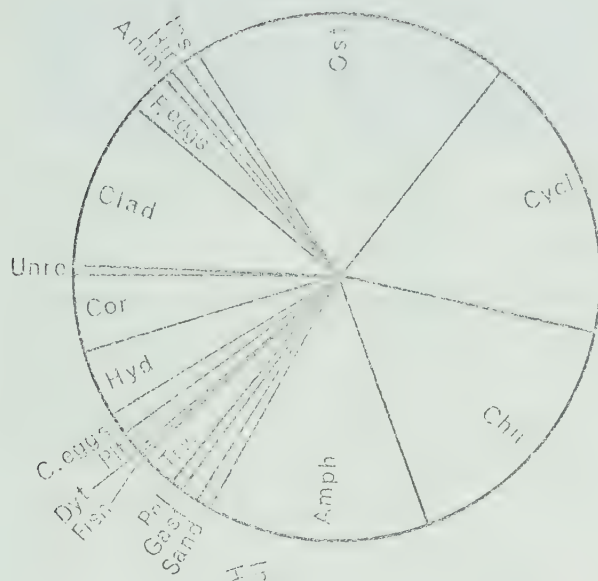
HIGH ISLAND



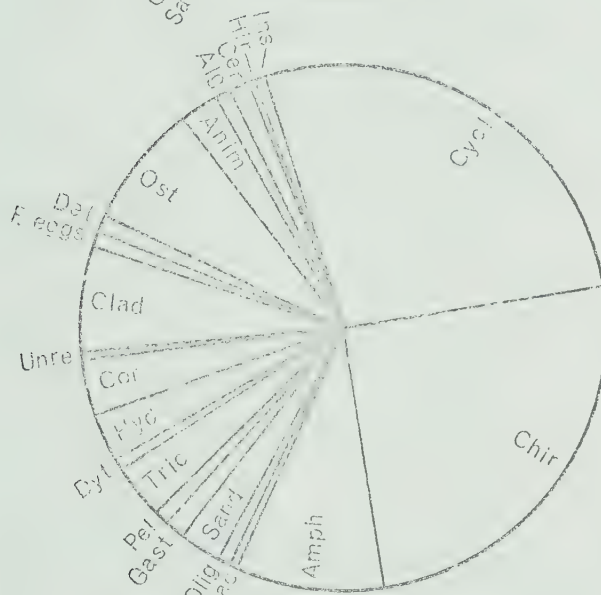
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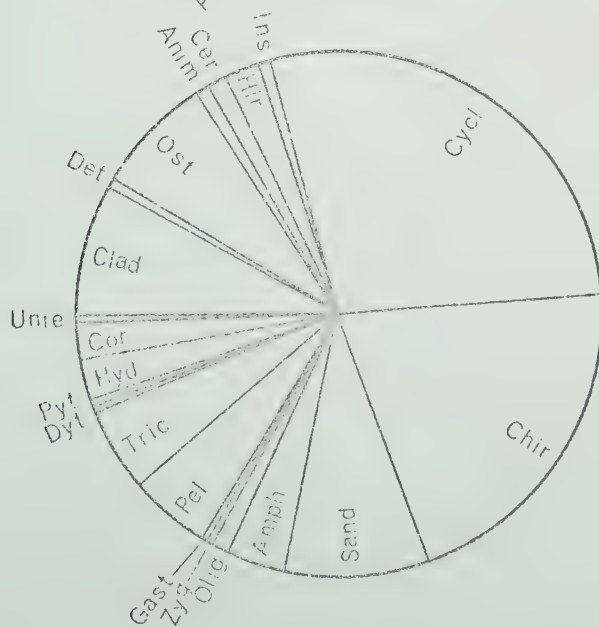
Fig. 6. A comparison of the three study areas in terms of total fish diet over a two-month period.



RESIDENCE POINT



HIGH ISLAND



YOUTH HOSTEL BAY

Table 4. The occurrence of food organisms as stomach contents of fish collected at the three study areas on four dates. Residence Point, High Island, and Youth Hostel Bay are represented by the letters X, Y, and Z respectively. 'Unidentified' and 'Unrecognizable' categories have been omitted.

Diet Item	June 9	June 30	July 21	Aug. 11
Chironomidae larvae	X Y Z	X Y Z	X Y Z	X Y Z
Cyclopoida nauplii	X Y Z	X Y Z	X Y Z	X Y Z
Ostracoda	X Y Z	X Y Z	X Y Z	X Y Z
Amphipoda	X Y Z	X Y Z	X Y Z	X Y Z
Cladocera	X Z	X Y	X Y Z	X Y Z
Corixidae	Y	Y Z	X Y Z	X Z
Trichoptera larvae	Y Z	Z	X Y Z	X Y Z
Sand	Y Z	Z	Z	X Y Z
Pelecypoda	Z	Z	Z	X Y Z
Oligochaeta	Z		Z	Y Z
Hirudinea	X Z	X Z	X Z	Y
Ceratopogonidae larvae	Y Z	Z		Y Z
Fish eggs	X Y	X		
Hydracarina	Z	Y Z	X Y Z	X Y
Dytiscidae larvae		Z	X Y	
Algae	Y			
Terrestrial Arachnida	Y			
Gastropoda		Z	Y	X Y
Detritus			Y	Y Z
Fish			X	
Culicidae eggs				X
Zygoptera nymphs				Z

areas on four dates is presented in Fig. 5 and Table 4.

Some of the interesting points of comparison are as follows:

-chironomid larvae, cyclopoid nauplii, ostracods, and amphipods were important at all three locations on all collection dates

-cladocerans, corixids, and trichopteran larvae were present on all dates, but not at all locations

-the occurrence of sand appears to coincide with the occurrence of trichopteran larvae and pelecypods

-pelecypods and oligochaetes were most important at Youth Hostel Bay

-hirudineans were apparently not as important at High Island as they were at the other locations

-mites appeared earlier in the diet in High Island and Youth Hostel Bay samples

-dytiscid larvae appeared as diet items for only a short time

The results for all samples from each location are totalled in Tables 5, 6, and 7, and compared in Fig. 6. Again, a complete analysis of each sample is given in Appendix A.

C) A COMPARISON OF THE DIETS OF MALES AND FEMALES

The total diet of all known males over 35 mm from the eight Residence Point samples is analyzed in Table 8. Table 9 is an analysis of the

diet of all known females over 35 mm from the same samples. A comparison of the two is presented in Fig. 7.

Apparently, there was very little difference in diet between the sexes as far as the major diet items were concerned. However, algae, culicid eggs, fish and pelecypods were not found in female stomachs, while sand grains and dytiscid larvae were absent in male stomachs.

D) A COMPARISON OF THE DIET OF LARGE AND SMALL FISH

Tables 8 and 9 are combined in Table 10 to present an analysis of the diet of all fish over 35 mm (standard length). The total diet of fish under 35 mm from the same samples is analyzed in Table 11. A comparison of the two is presented in Fig. 8. In Fig. 8, the diet of large fish appears to be more various than that of small fish, but this may be attributed to the larger sample size. A comparison of the diet of small fish with that of males or females might make the difference in diet between large and small fish more clear.

The diet of small fish consisted mostly of small organisms. Small fish exhibited a tendency to eat large numbers of the same small organism, while large individuals tended to eat a variety of organisms. Cyclopoid nauplii and cladocerans were significantly more important as diet items in small fish, whereas large organisms such as amphipods and large chironomids were less important. Hirudineans were notably absent in the stomachs of small fish. In fact, they were most common as diet items in fish over 50 mm. Ostracods were an important part of the diet for fish of all sizes.

E) THE DIET OF FRY

An analysis of the stomach contents of a group of fry under 20 mm (standard length), is presented in Fig. 9 and Table 12. Apparently, the

Table 5. The diet of the fish at Residence Point over a two-month period based on the stomach contents of 200 fish.

Diet Item	% Occurrence	% Number	% Volume Points
Amphipoda	13.98	5.50	22.33
Cyclopoida nauplii	17.71	35.57	19.35
Chironomidae larvae	16.08	5.37	15.71
Ostracoda	19.98	27.44	13.21
Cladocera	10.52	19.27	9.80
Corixidae	4.66	1.03	6.36
Trichoptera larvae	2.22	0.15	3.44
Hirudinea	0.93	0.11	1.97
Fish eggs	2.75	1.29	1.68
Unrecognizable material	0.37	-----	1.17
Culicidae eggs	1.20	2.92	0.78
Fish	0.27	0.01	0.74
Gastropoda	1.25	0.41	0.65
Hydracarina	4.02	0.76	0.64
Unident. Insecta	0.67	0.05	0.58
Unident. animal material	0.30	-----	0.46
Sand	0.94	-----	0.37
Pelecypoda	0.63	0.09	0.21
Unident. plant material	1.33	-----	0.19
Dytiscidae larvae	0.27	0.02	0.18

Table 6. The diet of the fish at High Island over a two-month period based on the stomach contents of 200 fish.

Diet Item	% Occurrence	% Number	% Volume Points
Cyclopoida nauplii	27.37	56.53	32.85
Chironomidae larvae	25.02	14.34	24.47
Amphipoda	8.11	4.25	13.79
Trichoptera larvae	3.75	1.97	7.43
Cladocera	6.51	11.27	4.62
Unident. animal material	2.22	-----	2.52
Corixidae	3.43	2.00	2.36
Ostracoda	7.86	3.57	2.28
Sand	3.89	-----	1.95
Fish eggs	0.80	3.68	1.41
Hirudinea	0.27	0.06	1.06
Unrecognizable material	0.54	-----	0.90
Ceratopogonidae larvae	1.21	0.43	0.86
Unident. Insecta	0.71	0.15	0.74
Pelecypoda	0.82	0.34	0.64
Detritus	1.10	-----	0.46
Hydracarina	3.26	0.74	0.44
Algae	0.80	-----	0.39
Terrestrial Arachnida	0.40	0.14	0.34
Gastropoda	1.10	0.53	0.27
Oligochaeta	0.54	-----	0.16
Dytiscidae larvae	0.28	0.01	0.09

Table 7. The diet of the fish at Youth Hostel Bay over a two-month period based on the stomach contents of 200 fish.

Diet Item	% Occurrence	% Number	% Volume Points
Cyclopoida nauplii	28.02	60.45	30.82
Chironomidae larvae	21.27	5.61	23.34
Gladocera	8.26	27.01	11.12
Trichoptera larvae	5.02	0.50	8.17
Hirudinea	1.91	0.14	6.61
Amphipoda	3.78	0.38	4.94
Ostracoda	7.40	4.15	3.47
Pelecypoda	4.97	0.64	3.23
Sand	8.60	-----	1.83
Corixidae	2.27	0.09	1.37
Ceratopogonidae larvae	1.19	0.14	1.05
Unident. animal material	0.89	-----	0.89
Unident. Insecta	0.87	0.05	0.76
Zygoptera nymphs	0.29	0.01	0.76
Oligochaeta	1.02	0.26	0.52
Hydracarina	2.66	0.49	0.28
Detritus	0.29	-----	0.21
Unrecognizable material	0.29	-----	0.18
Dytiscidae larvae	0.29	0.01	0.18
Unident. plant material	0.42	-----	0.16
Gastropoda	0.29	0.07	0.11

Fig. 7. A comparison of the diet of male and female fish based on the % occurrence figures given in Tables 8 and 9.



Table 8. The diet of male fish (over 35 mm) over a six-month period based on the stomach contents of 135 fish taken at Residence Point.

Diet Item	% Occurrence	% Number	% Volume Points
Amphipoda	19.47	6.16	26.74
Chironomidae larvae	20.35	7.69	25.29
Cyclopoida nauplii	18.58	59.94	20.25
Ostracoda	15.04	17.70	7.58
Corixidae	5.75	1.15	5.79
Trichoptera larvae	1.77	0.16	2.63
Hirudinea	0.89	0.06	2.41
Unident. animal material	1.33	-----	1.96
Fish	0.44	0.03	1.11
Cladocera	4.87	1.02	0.92
Fish eggs	1.77	0.83	0.84
Culicidae eggs	1.33	4.08	0.78
Pelecypoda	1.33	0.13	0.56
Detritus	0.89	-----	0.39
Hydracarina	2.21	0.70	0.28
Algae	0.89	-----	0.22
Unident. plant material	1.33	-----	0.17
Gastropoda	0.44	0.06	0.11

Table 9. The diet of female fish (over 35 mm) over a six-month period based on the stomach contents of 115 fish taken at Residence Point.

Diet Item	% Occurrence	% Number	% Volume Points
Cyclopoida nauplii	25.47	56.44	26.27
Chironomidae larvae	19.88	4.16	21.23
Amphipoda	12.42	4.16	19.11
Ostracoda	16.15	16.54	12.20
Cladocera	8.70	16.67	6.27
Corixidae	4.35	0.62	4.93
Unident. animal material	1.24	-----	1.94
Fish eggs	1.86	0.59	1.64
Trichoptera larvae	1.24	0.10	1.64
Unident. Insecta	1.24	0.03	1.42
Gastropoda	1.24	0.29	0.82
Detritus	1.24	-----	0.60
Unrecognizable material	0.62	-----	0.60
Hirudinea	0.62	0.10	0.45
Dytiscidae larvae	0.62	0.07	0.37
Hydracarina	1.86	0.23	0.22
Sand	0.62	-----	0.22
Unident. plant material	0.62	-----	0.07

Fig. 8. A comparison of the diet of large and small fish based on
Tables 10 and 11.

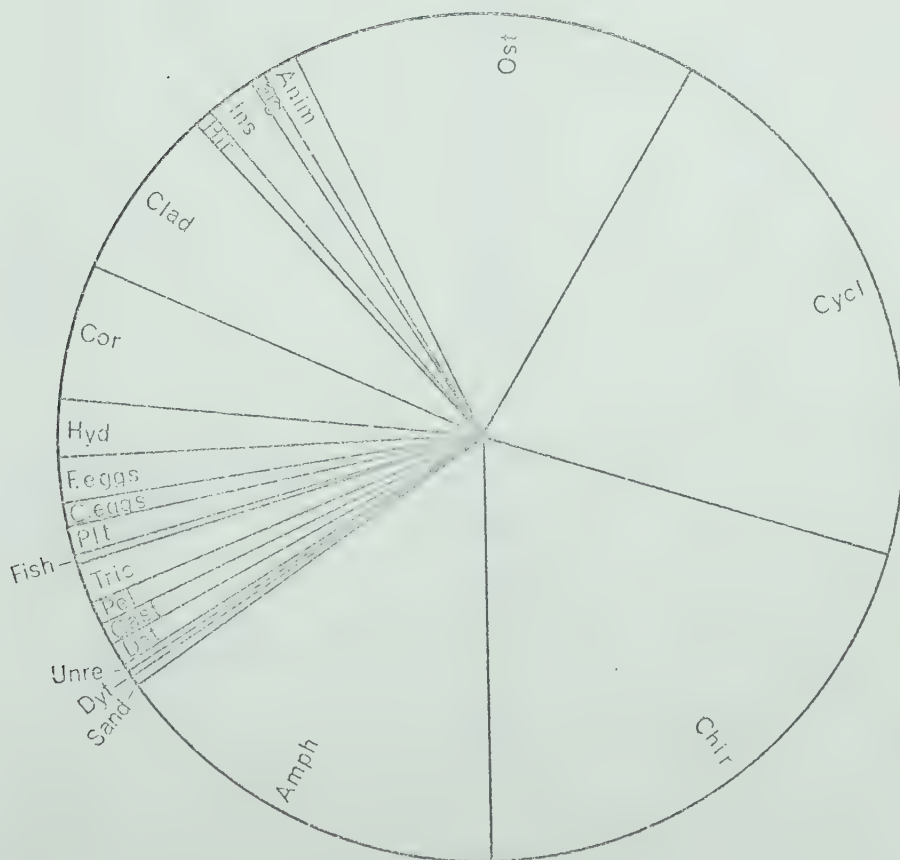
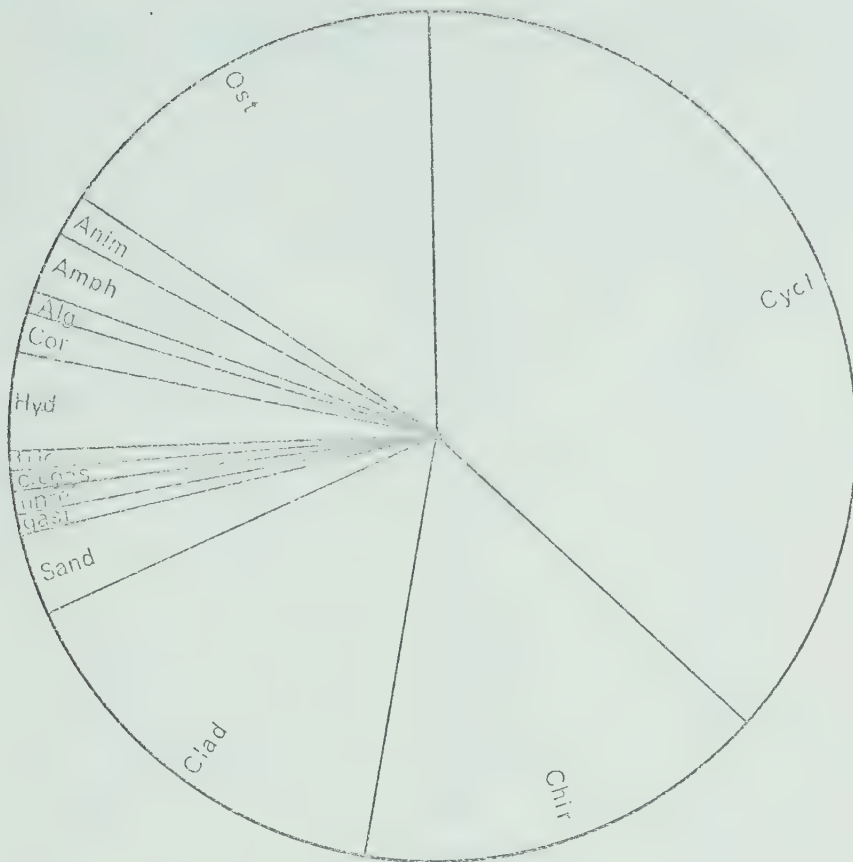


Table 10. The diet of fish over 35 mm over a six-month period based on the stomach contents of 250 fish taken at Residence Point.

Diet Item	% Occurrence	% Number	% Volume Points
Chironomidae larvae	20.16	5.95	23.55
Amphipoda	16.54	5.17	23.47
Cyclopoida nauplii	21.45	58.21	22.83
Ostracoda	15.50	17.13	9.56
Corixidae	5.17	0.89	5.42
Cladocera	6.46	8.74	3.21
Trichoptera larvae	1.55	0.13	2.21
Unident. animal material	1.29	-----	1.95
Unident. Insecta	1.29	0.16	1.95
Hirudinea	0.78	0.08	1.57
Fish eggs	1.81	0.71	1.18
Fish	0.26	0.02	0.64
Detritus	1.03	-----	0.48
Culicidae eggs	0.78	2.06	0.45
Gastropoda	0.78	0.18	0.42
Pelecypoda	0.78	0.06	0.32
Hydracarina	2.07	0.47	0.26
Unrecognizable material	0.26	-----	0.26
Dytiscidae larvae	0.26	0.03	0.16
Algae	0.52	-----	0.13
Unident. plant material	1.03	-----	0.13
Sand	0.26	-----	0.10

Table 10. The diet of fish over 35 mm over a six-month period based on the stomach contents of 250 fish taken at Residence Point.

Diet Item	% Occurrence	% Number	% Volume Points
Chironomidae larvae	20.16	5.95	23.55
Amphipoda	16.54	5.17	23.47
Cyclopoida nauplii	21.45	58.21	22.83
Ostracoda	15.50	17.13	9.56
Corixidae	5.17	0.89	5.42
Cladocera	6.46	8.74	3.21
Trichoptera larvae	1.55	0.13	2.21
Unident. animal material	1.29	-----	1.95
Unident. Insecta	1.29	0.16	1.95
Hirudinea	0.78	0.08	1.57
Fish eggs	1.81	0.71	1.18
Fish	0.26	0.02	0.64
Detritus	1.03	-----	0.48
Culicidae eggs	0.78	2.06	0.45
Gastropoda	0.78	0.18	0.42
Pelecypoda	0.78	0.06	0.32
Hydracarina	2.07	0.47	0.26
Unrecognizable material	0.26	-----	0.26
Dytiscidae larvae	0.26	0.03	0.16
Algae	0.52	-----	0.13
Unident. plant material	1.03	-----	0.13
Sand	0.26	-----	0.10

Fig. 9. The diet of fish under 20 mm based on the stomach contents of 18 fish taken at Residence Point on July 3, 1970.

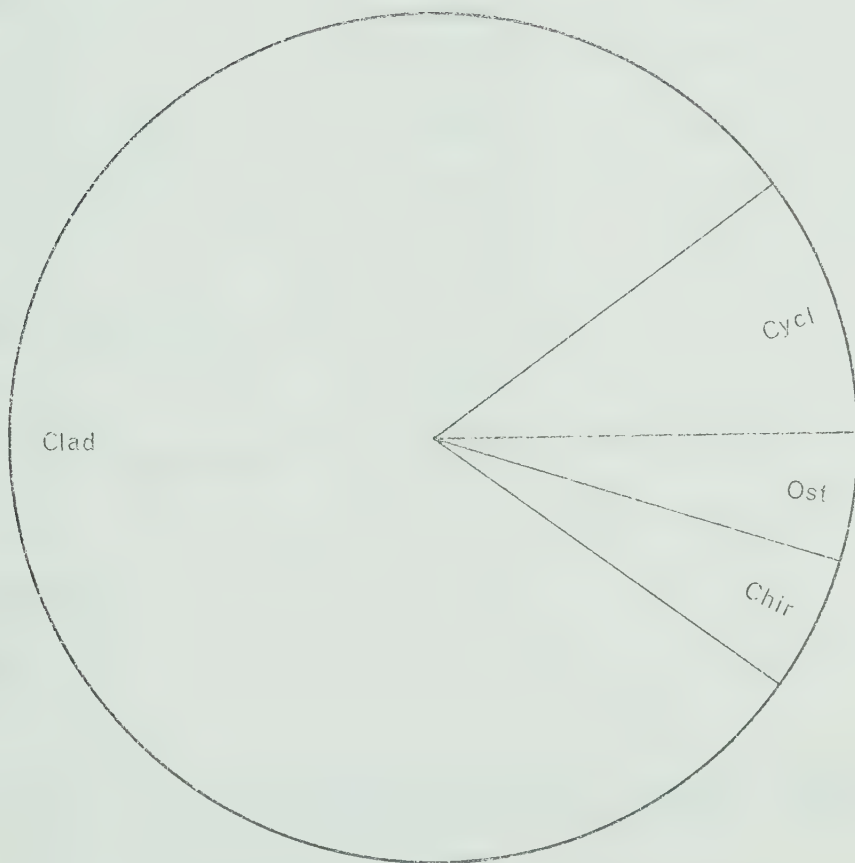


Table 11. The diet of fish under 35 mm over a six-month period based on the stomach contents of 103 fish taken at Residence Point.

Diet Item	% Occurrence	% Number	% Volume Points
Cyclopoida nauplii	36.96	74.34	47.37
Cladocera	16.67	18.51	18.54
Chironomidae larvae	15.94	2.16	14.18
Ostracoda	15.22	4.07	7.64
Amphipoda	2.17	0.40	2.80
Algae	0.72	-----	1.56
Trichoptera larvae	0.72	0.02	1.56
Corixidae	1.45	0.04	1.56
Unrecognizable material	0.72	-----	1.48
Sand	2.90	-----	1.09
Unident. animal material	1.45	-----	0.86
Hydracarina	3.62	0.26	0.66
Culicidae eggs	0.72	0.15	0.47
Gastropoda	0.72	0.04	0.23

Table 12. The diet of fish under 20 mm based on the stomach contents of 18 fish taken at Residence Point on July 3, 1970. *

Diet Item	% Occurrence	% Number
Cladocera	80.0	97.57
Ostracoda	5.0	0.49
Chironomidae larvae	5.0	0.16
Cyclopoida nauplii	10.0	1.78

* The occurrence of metacercaria of G. eucaliae as stomach contents was omitted since it seemed to be an atypical case.

diet of these fish consisted almost entirely of plankton. It was also apparent that these fish were eating large numbers of the same organism, in this case a cladoceran, Bosmina longirostris. Chironomids were the only definite bottom-dwelling organisms to form part of the diet, but their part was almost negligible in terms of the number eaten. Flukes of the trematode Gyrodactylus eucaliae Ikezaki and Hoffman, 1957 occurred as stomach contents in one fish, but this was considered a rare enough case to warrant the omission of this information in Fig. 9 and Table 12.

THE DIFFERENCE IN VERTICAL DISTRIBUTION ASSOCIATED WITH INFECTION BY Schistocephalus solidus (Muller, 1776).

METHOD

- A) In order to discover the significance of the difference in vertical distribution with respect to diet, the stomach contents of uninfected and infected fish were compared. Parasitized fish were collected with a dip net at the surface. Uninfected fish were collected with a seine net from the same location at the same time.
- B) The possibility that the sluggishness of the parasitized fish was associated with an infection by a parasite other than S. solidus was investigated. Thirteen fish infected with S. solidus were taken from a July 10, 1970 sample, and examined for the presence of Diplostomum baeri eucaliae Hoffman and Hundley, 1957 in the brain and eyes. Each fish had been exhibiting the behaviour in question, and had been collected separately with a dip net. The cranium of each fish was opened under water and the tissue teased apart under a dissecting microscope. Parasites were identified with the aid of a Vickers compound microscope.
- C) Since the possible effect of D. baeri eucaliae on the fish's behaviour was suggested by Mr. W. Bethel, his data (Bethel 1969 unpub)

concerning fish taken from Astotin Lake in the fall of 1969 were re-examined for any correlation between infection by D. baeri eucaliae and infection by S. solidus. A Chi-Square test for statistical significance was done, using a 2 x 2 contingency table.

D) In order to discover whether there was any difference in density between infected and uninfected fish, the following experiment was performed: Healthy and parasitized fish were collected from Astotin Lake on July 22, 1970, and placed in an aquarium for about 24 hours. Eighteen live uninfected fish were placed in a flask containing water. The increase in weight was recorded, and the amount of water displaced was measured. Density was calculated using the formula: density equals mass / volume. The density of 18 live parasitized fish, and the density of the 18 parasites removed from them was calculated in the same way. A parasite index was also calculated, using the figures obtained.

E) It was not possible to repeat the experiment in 1971 with fish from Astotin Lake, but a similar situation was found to exist in Half Moon Lake, which is about 16 km west of Vimy, Alberta. Sixty parasitized fish and 50 uninfected fish from Half Moon Lake were arranged in groups of 10, and the average densities for each group were calculated using the above method. Parasite density was calculated using two groups of 10 parasites, and one group of 41.

RESULTS

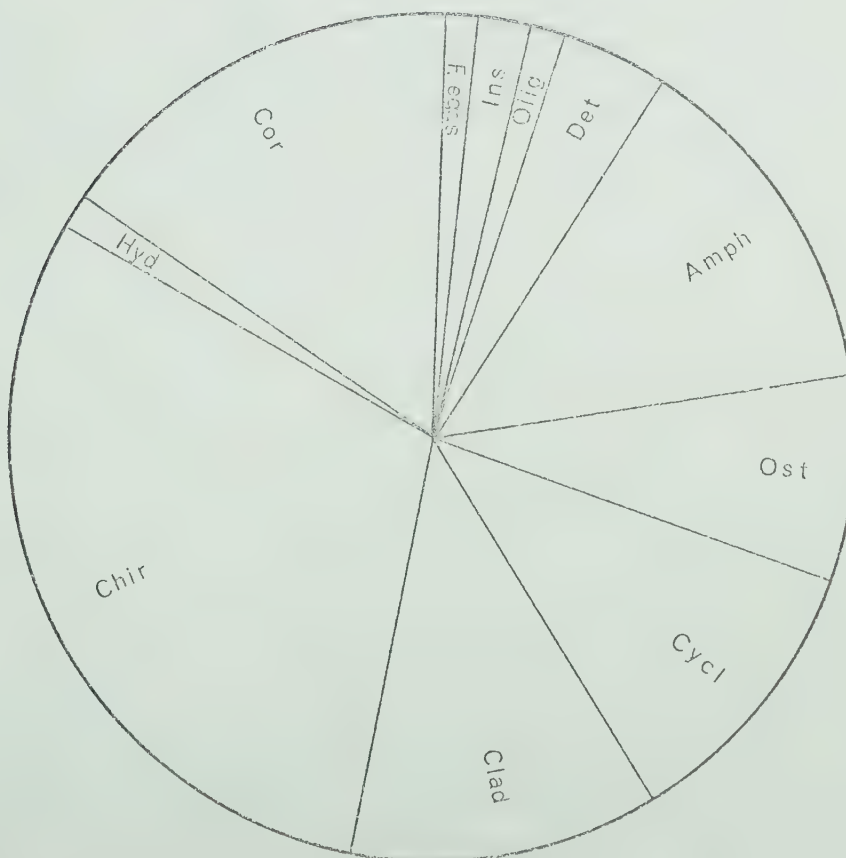
A) The diets of fish infected by S. solidus and uninfected fish are compared in Table 13 and Fig. 8. Most of the parasitized fish contained only one plerocercoid larva. Occasionally, two were present.

Apparently, corixids, mites, and cladocerans were more important diet items for parasitized fish than for uninfected ones, whereas chironomid larvae, cyclopoid nauplii, ostracods, and amphipods were more

Fig. 10. A comparison of the relative importance of diet items in parasitized and uninfected fish expressed in terms of frequency of occurrence.



PARASITIZED



UNINFECTED

Table 13. A comparison of the relative importance of diet items in parasitized and uninfected fish based on the stomach contents of 38 parasitized fish and 50 uninfected fish collected on July 3, 1970.

Diet Item	% Volume Points		% Number		% Occurrence	
	Uninf.	Para.	Uninf.	Para	Uninf.	Para
Corixidae	17.45	38.73	5.73	4.11	15.79	34.54
Hydracarina	0.53	1.90	1.05	0.47	1.32	5.45
Chironomidae larvae	34.27	2.11	13.45	0.24	30.26	3.64
Cladocera	15.86	54.53	54.39	94.92	11.84	43.64
Cyclopoida nauplii	5.11	0.21	10.06	0.24	10.52	3.64
Ostracoda	3.35	0.84	4.91	0.28	7.89	5.45
Amphipoda	15.68	1.68	4.33	0.24	13.16	3.64
Detritus	2.12	-----	-----	-----	3.95	-----
Oligochaeta	1.23	-----	0.12	-----	1.32	-----
Unident.Insecta	0.88	-----	0.70	-----	2.63	-----
Fish eggs	3.52	-----	5.26	-----	1.32	-----

important for uninfected fish. Detritus, oligochaetes, insect legs, and fish eggs were absent in the stomachs of parasitized fish, but present in the stomachs of some of the uninfected fish.

B) Of the fish examined for D. baeri eucaliae, the average size was 36.3 mm (SD 4.1), and the average number of S. solidus plerocercoids/ fish was 1.15. All spine types were represented. Only two of the fish (15.4%) were found to be infected with D. baeri eucaliae. The brain of one fish contained five metacercaria, the brain of the other contained one.

C) The data for 1969 to be re-examined comprised 22 fish, 10 of which were infected by S. solidus, and nine of which were infected by D. baeri eucaliae. Three fish were infected by both parasites, and six were uninfected. Using a contingency table and Yates' correction for small sample size, a Chi-square value of 0.2648 was calculated. At the 5% level of accuracy, with one degree of freedom, the tabled value (Bailey 1959) is 3.841. Therefore, no correlation between the presence of one parasite with the other is indicated.

D) When placed in the aquarium, the fish stratified themselves almost immediately, and maintained the same difference in vertical distribution noticed in the lake. Parasitized fish stayed near the surface, and healthy fish stayed close to the bottom.

The total density of the uninfected fish was 1.04 gm/ml. The total density of the infected fish was 1.03 gm/ml, and the total density of the parasites was 1.01 gm/ml.

A parasite index (P.I.) was calculated according to the formula:

$$P.I. = \frac{\text{Total weight of parasites}}{\text{Total weight of host plus parasites}} \times 100$$

A P.I. of 50 would indicate that the total weight of parasites was equal to the net weight of the host. The P.I. for parasitized fish from Astotin Lake was 19.37.

E) Of the fish from Half Moon Lake, only one of the 60 parasitized fish contained more than one plerocercoid. In that case, the second worm was much smaller than the first.

Of the five groups of 10 uninfected fish, the mean density was 0.981 gm/ml (SD 0.018). Of the six groups of 10 parasitized fish, the mean density was 1.017 gm/ml (SD 0.034). Of the two groups of 10 parasites and the one group of 41 parasites, the mean density was 1.145 gm/ml (SD 0.097).

INFECTION IN SMALL FISH BY Gyrodactylus eucaliae Ikezaki and Hoffman, 1957.

METHOD

An entire sample of fry from July 3, 1970, consisting of 116 fish was examined carefully under an Olympus binocular dissecting microscope in a search for ectoparasites. Particular care was taken in the examination of the gills of each fish.

RESULTS

Of the 116 fish examined, all between 8 mm. and 19 mm. (standard length), 6 were found to be infected with G. eucaliae. In each case, the flukes were concentrated on the undersurface of the fish. No parasites were found on the gills or fins. Flukes were not found on any fish larger than 15 mm.

DISCUSSION

PHYSICAL AND CHEMICAL DATA

The values for pH, alkalinity, and hardness are similar to those given by Lin (1968) for the summers of 1966 and 1967. These chemical

levels appear to have been relatively constant throughout the summer of 1970. The small fluctuations may simply be a reflection of inaccuracy in measurement.

Oxygen gradually decreased during the summer, but never dropped below 5 ppm, as it did in 1967. Lin (1968) attributed the drop in oxygen in 1967 to the death and subsequent decay of algae which had formed an extensive bloom. In the summer of 1970, the general decline in the amount of dissolved oxygen is probably attributable to a combination of increasing temperatures (Ruttner 1963) and increasing accumulations of decaying organic material. Local effects such as the occurrence of living algal blooms or an abundance of living submergents are probably responsible for the small peaks in dissolved oxygen. Unusually frequent winds may have helped maintain the high oxygen level (Smiley 1972).

THE INVERTEBRATE FAUNA

The difficulty of obtaining a reliable quantitative estimate of the relative abundance of invertebrates in a lake is well-known among limnologists (Hynes 1950).

Although sampling was consistent, the numbers of invertebrates collected were too small to be statistically meaningful, except perhaps in terms of totals. Because of this, a quantitative comparison of the invertebrate faunae of the three locations was not attempted. Hynes (1950) suggested that an ideal approach might be to gather as many invertebrates as possible, and treat them as stomach contents of a giant fish. The use of a volume - points method would eliminate the necessity for actual counts of large numbers of organisms, and would make possible a direct comparison between available food organisms and fish stomach contents. Such a comparison was not possible in this study because of the

incomplete and unreliable nature of the data. However, where macroplankton and definite bottom-dwelling organisms are concerned, the figures in Table 1 are probably a reasonably good reflection of relative availability. For example, the importance of chironomid larvae as diet items can probably be attributed to their availability in relatively large numbers. In contrast, such important diet items as cyclopoid nauplii and cladocerans are notably absent in Table 1. This is a reflection of the inadequacy of the Birge cone net, which yielded almost no results.

According to Table 1, the most abundant invertebrates in Astotin Lake during the summer of 1970 were chironomid larvae, whereas most other insects were restricted in both number and variety. Pennak (1953) suggested that this situation is typical for shallow North American Lakes with a pH value exceeding 9.0.

The differences between the lists of invertebrates collected in 1970 and 1971 point out the difficulty in completing such a list. No doubt, some of the invertebrates collected only in 1971 were also present in the lake in 1970. However, the situation was different in 1971, in that there were few fish in the lake. This may have allowed some invertebrates to become more abundant, since they were not being as heavily predated by fish. For example, dytiscid larvae were not observed in the lake until 1971, yet they did occur as fish stomach contents in 1970. On the other hand, adult mites were observed in 1970, but were never found as stomach contents or in invertebrate collections that year.

Particular invertebrates will be dealt with in subsequent sections in terms of their significance as diet items.

THE DIET OF THE BROOK STICKLEBACK

A) SEASONAL VARIATION IN DIET

Adult mites, adult dytiscids, and adult gastropods were the only organisms occurring in invertebrate samples but not in fish stomachs. Adult mites, usually red in colour, are probably distasteful to the fish, and the fish may have learned by association to avoid them (White 1918). Adult dytiscids and gastropods are probably not eaten because of their size, and perhaps also because of the hardness of their shells. With the exception of these organisms, it appears that all aquatic invertebrates are potential food for brook sticklebacks, and are exploited as such when available. Therefore, it seems reasonable to suppose that seasonal variation in the diet of these fish is a good reflection of seasonal changes in the invertebrate composition of the lake. The absence of particular organisms in fish stomachs during any part of the year is probably an indication and result of their absence in that part of the lake at that time. For example, dytiscid larvae are not present as stomach contents in early autumn probably because they have emerged to assume their terrestrial pupal stages (Pennak 1953).

The importance of chironomid larvae, cyclopoid nauplii, amphipods, and ostracods as diet items from April 30 to October 17 is probably directly related to their availability in relatively large numbers throughout this period.

The late appearance of corixids and mites at Residence Point may correspond to a late hatching time. Statements concerning the breeding season of mites vary widely, but some authorities maintain that the eggs are usually deposited in May, June, and July (Pennak 1953). This may account for the absence of mites as stomach contents in the early summer.

Cladocerans are subject to cyclical bursts in numbers (Ruttner 1963), and their absence in early summer may be a reflection of this, or it may be a reflection of a delayed hatching time due to unsuitable temperatures.

Culicid and fish eggs obviously form part of the diet only when they are present, and their occurrence as diet items matches perfectly their occurrence in the lake.

The absence of pelecypods in fish stomachs during the early part of the summer might be explained by their mode of reproduction. In the Sphaeriidae, the young are retained in the body of the adult for some time. According to Pennak (1953), "reproduction is thought to continue through the year, although very few young are released during the winter months."

The absence of gastropods during the early part of the summer is not easily explained. Oviposition usually occurs in the spring in freshwater gastropods and some exhibit seasonal migrations, moving into deeper water (where the fish were) as the summer progresses (Pennak 1953).

Pupation is short in trichopterans and usually occurs in late spring or early summer (Pennak 1953). From this, it can be assumed that most trichopterans are existing in the form of eggs until later in the summer, which may explain why they were not part of the diet until then.

B) A COMPARISON OF DIET AT THE THREE STUDY AREAS

Chironomid larvae, cyclopoid nauplii, ostracods, and amphipods were found as stomach contents on all collection dates and at all three study areas. These organisms were numerous and widespread in the lake, and constituted a major portion of fish diet throughout the summer, probably as a result of their availability. Cladocerans and corixids were not as consistent as diet items as the above, probably because they were not as randomly distributed in the lake.

There is a very interesting correlation between the occurrence of trichopteran larvae and the occurrence of sand in fish stomachs (Table

4). The trichopterans involved, Oecetis and Molanna, build their cases of sand. Evidently, a fish takes in a certain amount of sand whenever it eats one of these caddis fly larvae. In the two instances (July 21) when trichopterans occurred without sand, the insects proved to be phryganeids, which generally use vegetable matter in the construction of their cases in Astotin Lake.

Geratopogonid larvae, pelecypods and oligochaetes were most common at Youth Hostel Bay. This bay has a sand bottom, suitable for such organisms, but plenty of wave action. These organisms are perhaps more oblivious to wave action than some of the others. Culicid eggs, for example, were found only at Residence Point, the most sheltered of the study areas.

Fish eggs were not found as stomach contents at Youth Hostel Bay. This is probably because there were fewer nests at this location because of the wave action and the lack of rooted aquatic plants.

Hirudineans do not seem to have been very abundant at High Island. Neither do they seem to have been diet items of much importance, yet hirudineans were often observed there, sometimes protruding from the mouths of living and dead fish.

Mite instars, not adults, were quite common as diet items at all three study areas, but usually occurred in small numbers. The adult mites in Astotin Lake are either completely red or have some red in their color pattern, and are probably distasteful as well (White 1918). On one occasion, a stickleback was observed to catch an adult mite, then spit it out. In aquaria, adult mites appeared to be ignored by the otherwise curious sticklebacks.

The instance of cannibalism was apparently a rare case, since it only occurred once in the entire group of fish examined (about 1200 fish).

Occurrences of terrestrial arachnids and zygopteran nymphs are also apparently rare.

C) A COMPARISON OF THE DIETS OF MALES AND FEMALES

Apparently, there is very little difference in diet between the sexes, in spite of the difference in distribution during the breeding season. Comparisons of male and female diet on particular dates during the breeding season, and in the totals given in Tables 8 and 9 revealed no major differences.

Fish eggs occurred in the stomachs of fish of both sexes. The possibility exists that males were performing a useful function by removing diseased eggs from their own nest. Since the males exhibit parental care, it seems unlikely that they would eat the same eggs they were protecting for any other reason, yet it was a male that was involved in the only case of cannibalism. Females, on the other hand, are not involved in caring for the eggs.

Algae, culicid eggs, pelecypods and fish did not occur in female stomachs, while dytiscid larvae and sand did not occur in male stomachs. These items probably would have occurred in the stomachs of both male and female fish had the sample size been larger. With the exception of fish, all of these items were found in stomachs of fish of both sexes in samples not used in this comparison.

The lack of sand in the stomachs of males used in this comparison may be associated with the lack of non-phryganeid trichopterans in their stomachs.

D) A COMPARISON OF THE DIET OF LARGE AND SMALL FISH

The diet of small fish consisted mostly of small organisms such as cyclopoid nauplii, ostracods, and cladocerans. Neither the method of fish

collection (seining), nor the occurrence of the above organisms as diet items for small fish suggests a strictly benthic or planktonic feeding habit, or a difference in vertical distribution between large and small fish. It seems more reasonable to suppose that large and small fish were feeding in the same area, but that the variety of potential food was restricted by the size of the fish's mouth and stomach. This contention is supported by the fact that the same organisms were also eaten in great numbers by large fish. However, large fish ate, in addition to the above organisms, a great many large organisms such as amphipods, corixids, unidentified insects, hirudineans and even another fish in one case.

It was observed that large individuals tended to have more variety in their diet than small ones. This may be related to the fact that mouth size is not as restricting to a large fish. It may also be related to the possibility that the successful pursuit of some food organisms requires a degree of skill and coordination not yet acquired by the young fish.

E) THE DIET OF FRY

The diet of the fry examined consisted primarily of cladocerans. Cyclopoid nauplii, ostracods, and chironomids were present in fewer numbers and in fewer cases. Flukes of Gyrodactylus eucaliae Ikezaki and Hoffman, 1957 were present in the stomach of one fish. Both the method of collection (dip-netting at the surface), and the predominance of cladocerans as stomach contents suggests a planktonic feeding habit. The fact that schools of fry, herded by males, were often observed near the surface supports this contention. Apparently, the diet of fry is a good reflection of their distribution.

None of the food items were large. The size of the mouth in these fish necessarily restricts their diet to small organisms. The apparent tendency for small fish to eat large numbers of the same organism is

evident in the case of these fry, since most of their food consisted of one species of cladoceran, Bosmina longirostris. This may be related to a restricted availability of food corresponding to the limitations in movement imposed on the fry by the male.

The inclusion of the single occurrence of G. eucaliae flukes in the results on the diet of fry would probably have resulted in a distorted picture of the normal diet of the brook stickleback.

THE DIFFERENCE IN VERTICAL DISTRIBUTION ASSOCIATED WITH INFECTION BY Schistocephalus solidus (Müller, 1776)

A) The pattern of infection in C. inconstans in Astotin Lake appears to differ from that in Gasterosteus aculeatus Linneaus in that there are generally fewer worms per fish.

With regard to differences in diet between uninfected and infected fish, it was found that cladocerans, corixids, and mites were the important diet items for parasitized fish, while chironomid larvae, cyclopoid nauplii, ostracods, and amphipods were the important diet items for unparasitized fish. Most of these differences in diet can be explained in terms of differences in availability of food organisms.

The cladocerans were identified as Bosmina longirostris, which is one of the common open water and limnetic forms (Pennak 1953). These were the most significant diet item for parasitized fish, and so it would appear that the parasitized fish were feeding heavily near the surface. In contrast, chironomid larvae, which are usually confined to the bottom, were the most significant food item for uninfected fish. Thus, it appears that the diet of parasitized fish is a reflection of their position near the surface. The absence of detritus and oligochaetes in the stomachs of parasitized fish supports this contention.

Surprisingly, amphipods and cyclopoid nauplii were more important as diet items for uninfected fish. But, according to Pennak (1953),

"as a group, amphipods are strongly thigmotactic and react negatively to light. Consequently, during the daytime they are in vegetation or hidden under and between debris and stones." If this were true for the amphipods in Astotin Lake, they would be much less available to fish feeding at or near the surface. Similarly, cyclopoid nauplii are not necessarily planktonic. Many cyclopoids are restricted to bottom debris (Pennak 1953), and those in Astotin Lake could easily be among them.

Most of the other organisms were probably equally available in the water column, but differences in diet concerning these organisms were not striking.

It might be argued that differences in diet between uninfected and infected fish are a result of the impaired efficiency in swimming in parasitized fish. This would not explain the absence of fish eggs, detritus, or oligochaetes in the stomachs of parasitized fish. Neither would it explain the lesser importance of such slow organisms as cyclopoid nauplii and ostracods as diet items for parasitized fish, or the greater importance of organisms such as corixids, which appear to be among the most difficult food organisms to capture.

For whatever reason parasitized fish are situated close to the surface, it appears that their diet is restricted by the availability of food organisms in the upper strata of the water.

B) Only 15.4% of the fish examined were infected by Diplostomum baeri eucaliae, yet all of the fish had been collected at the surface. Since all fish were infected by Schistocephalus solidus, and all were exhibiting the behaviour in question, it appears that S. solidus is solely responsible for the difference in vertical distribution and behaviour.

The number of worms per fish were six and one. Hoffman and Hundley (1957) reported an 82% infection in a sample of 62 fish from North

Dakota, with as many as 335 metacercaria in the brain of one fish. However, Hoffman and Hoyme (1958) noted no impairment of reflexes in their experiences with the infection.

The snail, Stagnicola palustris was named as host by Hoffman and Hundley (1957) for D. baeri eucaliae. Although invertebrate collections made in 1970 and 1971 failed to reveal the presence of this snail in the lake, it has previously been found there (Kevan 1970), and is probably still present.

C) There was no correlation between the presence of S. solidus and D. baeri eucaliae according to the re-examined data from 1969. Therefore, it seems unlikely that the presence of one parasite affects the susceptibility of the fish to the other, or that D. baeri eucaliae is in any way responsible for the observed difference in vertical distribution and behaviour.

D) The immediate separation of infected and uninfected fish placed in aquaria suggested a mechanical cause for the difference in vertical distribution rather than a preference in parasitized fish for a different oxygen or temperature level.

The parasitized fish were found to be less dense than the uninfected fish, and the parasites themselves were found to be even less dense. The inclusion in the body of a fish of a parasite less dense than itself would result in a lowering of the overall density of the fish. Since the brook stickleback has an air bladder which is compressible, a decrease in density could result in the fish's becoming more positively buoyant. A fish which is positively buoyant at the surface would have difficulty swimming to a depth of even a few feet. For a fish to regain neutral buoyancy, a reduction in the size of the air bladder would have to occur. As observed by Arme and Owen (1966), no reduction in the size of the air

bladder was discernible in fish infected by S. solidus.

More than half of the fish (G. aculeatus) examined by Arme and Owen (1966) had a P.I. greater than 25, as compared to an average of 19.37 for the fish (G. inconstans) from Astotin Lake.

E) The desirability of more data to support the hypothesis that a density difference between uninfected and infected fish was causing the difference in vertical distribution prompted the examination of the fish from Half Moon Lake. However, the results did not support the hypothesis. Uninfected fish were found to be less dense than parasitized fish, which were, in turn, found to be less dense than the parasites themselves. The small values for standard deviation suggest that these results are statistically reliable. However, the hypothesis does not necessarily have to be discarded. The fish from Half Moon Lake were subjected to a great temperature change when brought back to the laboratory. In fact, there was some ice on the lake at the time of collection. This temperature increase would have resulted in air bladder expansion. Air bladder expansion would have been more severe for uninfected fish, which were collected from a depth of about 1.5m. This increase in air bladder size could have been enough to render the uninfected fish less dense than water. The effect would not have been quite as striking in the parasitized fish, since the inclusion of the now more dense parasites would have contributed to a greater overall density for the fish. The greater density of the parasites in the fish at Half Moon Lake is difficult to explain, but the effect of this difference on the fish is not. It should be noted here that the parasitized fish at Half Moon Lake were distributed differently from the healthy fish in that they were in the shallows and relatively easy to catch. However, these fish were not at

the surface as they were in Astotin Lake, but rather on the bottom, although at shallow depths.

Therefore, it seems that the hypothesis is still a viable one, but that further research is required. Difficulties with the changeability of air bladder size could be overcome either by removing all air bladders or by acclimatizing all fish to the same depth and temperature prior to density calculations. The latter set of conditions were much more closely approximated with the fish from Astotin Lake.

INFECTION IN SMALL FISH BY Gyrodactylus eucaliae Ikezaki and Hoffman, 1957.

Of the fish examined for G. eucaliae, 5.2% were found to be infected. Flukes were not found on fish over 15 mm.

Death by gyrodactyliasis is known to occur in goldfish, Carassius auratus (Linnaeus), rainbow trout, Salmo gairdneri Richardson, and the black bullhead, Ictalurus melas (Rafinesque). Death is thought to be attributable to interference with gill surfaces by large populations of the flukes. Since the parasites found in this study appeared to be confined to the undersurface of the small fish, there is no suggestion of fatal gyrodactyliasis by suffocation.

Since the parasites were discovered as the stomach contents of one fish, there is the suggestion of a possible mutual cleaning activity among the fish. However, it seems more likely that the occurrence was purely accidental. Small fish often eat large numbers of the same small organism, and the availability of Gyrodactylus flukes as food is probably a rare occurrence.

CONCLUSIONS

1. The brook sticklebacks of Astotin Lake are almost entirely carnivorous. Chironomid larvae, cyclopoid nauplii, amphipods, and ostracods

were consistently the most important diet items throughout the study period. With the exception of adult mites, adult gastropods, and adult dytiscids, all the aquatic invertebrates in Astotin Lake are potential food for these fish and are eaten when available. Presumably, adult mites are not eaten because some or all of them are distasteful to the fish. Adult dytiscids and gastropods are probably not eaten because of their size or the hardness of their exterior coverings.

2. Differences in diet between fish from different study areas can be attributed to differences in the relative availability of certain food organisms. Differences in bottom type, the extent of wave action, and the amount of vegetation are probably responsible for differences in the invertebrate fauna, since temperature and chemical conditions were practically the same at all three study areas. Similarly, differences in diet associated with time of year are a reflection of the availability of the various food organisms.

3. There is a difference in diet between large and small fish which is probably attributable to the difference in mouth and stomach size, rather than a distributional difference. The small fish generally ate large numbers of the same small organism, and never ate large organisms. The large fish ate both small and large organisms, and were more inclined to eat a mixture of organisms than the small fish. However, the diet of recently-hatched fry may be a reflection of more than the possession of a small mouth. Young fry have a restricted distribution near the surface which is imposed upon them by the guardian male. This may explain why their diet consists primarily of planktonic organisms.

4. There is virtually no difference in diet between males and females, in spite of distributional differences during the breeding period. Fish eggs were eaten by members of both sexes.

5. The diet of fish infected with S. solidus consists primarily of planktonic organisms. Since these fish are generally restricted to the upper strata of the water, the availability of food organisms is limited for them, and their diet is a good reflection of their vertical distribution.
6. C. inconstans is capable of cannibalism, but this is apparently a rare case.
7. Sand is not deliberately eaten by the fish, but is accidentally ingested while trichopteran larvae with sand cases are being eaten.
8. Hirudineans were often found in the stomachs of large fish, in various stages of digestion. However, attempts to eat hirudineans sometimes resulted in the death of both the fish and its prey.
9. S. solidus is solely responsible for the difference in vertical distribution and behaviour exhibited by infected fish. That the difference in vertical distribution is associated with a difference in buoyancy between infected and uninfected fish is still an interesting possibility, but further research is required.
10. An accurate estimate of the incidence of infection by S. solidus was made difficult by the peculiar distribution of the infected fish. However, it can be stated that there was usually one plerocercoid per fish, and that there was an average P.I. value of 19.37 for these fish. There were more females than males among fish infected with S. solidus.
11. Many of the brook sticklebacks in Astotin Lake were parasitized by one or more of the following:

-Gyrodactylus eucaliae Ikezaki and Hoffman, 1957
(found only on the ventral surface of fish under 20 mm)

-Diplostomum baeri eucaliae Hoffman and Hundley, 1957

-an unidentified microsporidean

-an unidentified encysted trematode

12. Spine number was apparently unrelated to differences in susceptibility to infection by S. solidus.

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Appendix A. Complete data for all samples used in sex, size and location comparisons, and in the analysis of seasonal variation. Each sample consisted of 50 fish.

RESIDENCE POINT
APRIL 31

Diet Item	% Number	% Volume	% Occurrence
Chironomidae larvae	28.13	59.54	43.14
Cyclopoida nauplii	56.88	14.71	25.49
Unident. animal mat.	-----	7.13	5.88
Ostracoda	13.76	7.13	17.65
Algae	-----	4.59	1.96
Hirudinea	0.31	4.14	1.96
Unident. Insecta	0.31	2.30	1.96
Ceratopogonidae larvae	0.61	0.46	1.96

MAY 22

Diet Item	% Number	% Volume	% Occurrence
Cyclopoida nauplii	96.88	73.62	60.65
Chironomidae larvae	1.17	18.16	21.31
Unident. Insecta	0.17	3.68	3.28
Ostracoda	1.74	2.70	8.20
Amphipoda	0.04	0.86	3.28
Detritus	-----	0.61	1.64
Algae	-----	0.37	1.64

JUNE 9

Diet Item	% Number	% Volume	% Occurrence
Cyclopoida nauplii	73.31	47.41	38.81
Amphipoda	4.27	28.62	16.42
Ostracoda	17.91	9.05	22.39
Unrecognizable	-----	4.66	1.49
Hirudinea	0.12	4.31	1.49
Fish eggs	3.20	2.76	7.46
Unident. Insecta	0.12	1.55	1.49
Chironomidae larvae	0.83	1.47	8.96
Cladocera	0.24	0.17	1.49

JUNE 30

Diet Item	% Number	% Volume	% Occurrence
Chironomidae larvae	13.30	32.34	23.53
Corixidae	3.54	21.15	12.94
Ostracoda	36.36	15.10	18.82
Cyclopoida nauplii	25.34	9.20	11.76
Amphipoda	3.70	8.58	9.41
Fish eggs	1.94	4.75	3.53
Cladocera	4.04	2.60	8.23
Culicidae eggs	10.77	2.14	3.53
Unident. animal mat.	-----	1.84	1.18
Hirudinea	0.25	0.92	1.18
Unident. Insecta	0.09	0.77	1.18
Hydracarina	0.67	0.61	4.71

JULY 21

Diet Item	% Number	% Volume	% Occurrence
Amphipoda	5.10	26.47	14.90
Cladocera	47.55	26.32	22.34
Cyclopoida nauplii	39.97	17.21	12.77
Chironomidae larvae	2.53	12.06	18.09
Trichoptera larvae	0.35	7.21	6.38
Fish	0.05	2.94	1.06
Hirudinea	0.05	2.65	1.06
Ostracoda	2.73	1.76	7.45
Corixidae	0.20	1.03	3.19
Hydracarina	1.37	0.88	6.38
Unident. plant mat.	-----	0.74	5.32
Dytiscidae larvae	0.10	0.73	1.06

AUGUST 11

Diet Item	% Number	% Volume	% Occurrence
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Ostracoda	52.24	26.94	31.25
Amphipoda	8.83	25.63	15.00
Chironomidae larvae	4.73	16.98	13.75
Cladocera	24.87	10.12	10.00
Trichoptera	0.25	6.53	2.50
Cyclopoida nauplii	2.99	3.59	7.50
Corixidae	0.37	3.27	2.50
Gastropoda	1.62	2.61	5.00
Sand	1.86	1.47	3.75
Hydracarina	1.00	1.47	3.75
Culicidae eggs	0.87	0.98	1.25
Pelecypoda	0.37	0.82	2.50

SEPTEMBER 1

Diet Item	% Number	% Volume	% Occurrence
Cladocera	84.45	65.21	45.95
Amphipoda	1.76	14.48	6.76
Cyclopoida nauplii	6.97	6.07	21.62
Ostracoda	5.07	5.60	9.46
Culicidae	0.78	2.80	1.35
Corixidae	0.26	1.95	2.70
Trichoptera	0.13	1.25	2.70
Chironomidae larvae	0.13	0.93	2.70
Unident. Insecta	0.06	0.78	1.35
Hydracarina	0.33	0.31	2.70
Gastropoda	0.06	0.31	1.35
Detritus	-----	0.31	1.35

OCTOBER 17

Diet Item	% Number	% Volume	% Occurrence
Cyclopoida nauplii	60.54	31.25	32.97
Chironomidae larvae	13.78	24.89	16.48
Amphipoda	7.84	19.57	17.58
Cladocera	15.67	9.19	12.09
Corixidae	0.81	5.49	6.59
Unident. Anim. Mat.	-----	4.98	3.30
Detritus	-----	1.37	2.20
Sand	-----	1.37	2.20
Pelecypoda	0.14	0.86	1.10
Ostracoda	1.08	0.69	4.40
Unident. Insecta	0.14	0.34	1.10

HIGH ISLAND
JUNE 9

Diet Item	% Number	% Volume	% Occurrence
Chironomidae larvae	16.38	27.42	25.39
Amphipoda	8.47	25.17	15.87
Trichoptera larvae	6.78	18.65	9.52
Fish eggs	14.69	5.62	3.18
Cyclopoida nauplii	36.72	4.72	17.46
Ostracoda	7.91	4.04	6.35
Sand	-----	3.37	7.94
Corixidae	7.34	2.92	3.18
Unident. Insecta	0.57	2.25	1.59
Unident. Anim. Mat.	----	1.80	3.18
Algae	-----	1.57	3.18
Terrestrial Arach.	0.57	1.35	1.59
Ceratopogonidae larv.	0.57	1.12	1.59

JUNE 30

Diet Item	% Number	% Volume	% Occurrence
Cyclopoida nauplii	94.27	82.39	51.85
Chironomidae larvae	0.77	7.04	18.52
Cladocera	4.13	3.10	6.17
Corixidae	0.08	3.10	4.93
Unident. animal mat.	-----	2.11	1.24
Hydracarina	0.40	0.70	8.64
Ostracoda	0.31	0.70	6.17
Unident. Insecta	0.02	0.70	1.24
Amphipoda	0.02	0.14	1.24

JULY 21

Diet Item	% Number	% Volume	% Occurrence
Cyclopoida nauplii	61.18	37.08	31.46
Chironomidae larvae	11.12	32.10	25.84
Cladocera	22.82	9.87	10.11
Unident. animal mat.	-----	6.18	4.49
Amphipoda	0.26	4.64	3.37
Ostracoda	3.74	3.43	13.48
Corixidae	0.57	3.43	5.62
Trichoptera larvae	0.16	2.58	1.13
Dytiscidae larvae	0.05	0.34	1.13
Detritus	-----	0.34	1.13
Hydracarina	0.05	-----	1.13
Gastropoda	0.05	-----	1.13

AUGUST 11

Diet Item	% Number	% Volume	% Occurrence
Chironomidae larvae	29.00	31.32	30.43
Amphipoda	8.22	25.19	11.96
Trichoptera larvae	0.91	8.47	4.35
Cyclopoida nauplii	33.56	7.20	8.70
Cladocera	18.04	5.50	9.78
Sand	-----	4.44	7.61
Hirudinea	0.23	4.23	1.09
Pelecypoda	1.37	2.54	3.26
Unrecognizable	-----	3.60	2.17
Ceratopogonidae larvae	1.14	2.33	3.26
Detritus	-----	1.48	3.26
Hydracarina	2.51	1.06	3.26
Gastropoda	2.06	1.06	3.26
Ostracoda	2.28	0.95	5.44
Oligochaeta	0.68	0.63	2.17

YOUTH HOSTEL BAY
JUNE 9

Diet Item	% Number	% Volume	% Occurrence
Cyclopoida nauplii	85.86	35.60	37.04
Trichoptera	1.30	20.80	8.64
Hirudinea	0.47	13.00	3.70
Chironomidae larvae	1.18	12.40	8.64
Amphipoda	0.47	5.40	4.94
Ostracoda	7.89	3.80	12.35
Ceratopogonidae larvae	0.35	3.20	2.47
Sand	-----	3.00	11.11
Unident. animal mat.	-----	1.00	1.13
Hydracarina	1.65	0.60	6.17
Pelecypoda	0.12	0.60	1.13
Oligochaeta	0.47	0.40	1.13
Cladocera	0.24	0.20	1.13

JUNE 30

Diet Item	% Number	% Volume	% Occurrence
Cyclopoida nauplii	90.95	52.20	39.77
Chironomidae larvae	7.20	25.25	23.86
Amphipoda	0.36	8.23	4.54
Hirudinea	0.06	7.09	2.27
Pelecypoda	0.89	2.41	6.81
Sand	-----	1.84	12.50
Dytiscidae larvae	0.03	0.71	1.14
Unrecognizable	-----	0.71	1.14
Gastropoda	0.27	0.43	1.14
Ostracoda	0.09	0.14	1.14
Corixidae	0.06	0.43	2.27
Trichoptera	0.03	0.43	1.14
Ceratopogonidae larvae	0.03	0.14	1.14
Hydracarina	0.03	0.00	1.14

JULY 21

Diet Item	% Number	% Volume	% Occurrence
Chironomidae larvae	10.32	31.13	31.67
Cladocera	63.10	28.74	16.67
Cyclopoida nauplii	23.47	13.51	16.67
Hirudinea	0.05	6.36	1.67
Pelecypoda	1.17	5.83	8.33
Trichoptera larvae	0.28	3.97	3.33
Corixidae	0.11	3.18	3.33
Amphipoda	0.22	2.38	3.33
Ostracoda	0.89	1.59	3.33
Oligochaeta	0.11	1.33	1.67
Sand	-----	0.79	5.00
Unident. plant material	-----	0.66	1.67
Hydracarina	0.28	0.53	3.33

AUGUST 11

Diet Item	% Number	% Volume	% Occurrence
Chironomidae larvae	3.75	24.60	20.93
Cyclopoida nauplii	41.67	21.96	18.60
Cladocera	44.76	15.46	15.12
Ostracoda	7.76	8.34	12.79
Trichoptera larvae	0.39	7.49	6.98
Pelecypoda	0.39	4.09	3.49
Amphipoda	0.46	3.75	2.33
Unident. Insecta	0.19	3.06	1.16
Zygoptera nymphs	0.06	3.06	1.16
Unident. animal material	-----	2.55	2.33
Corixidae	0.19	0.85	1.16
Sand	-----	1.70	5.81
Ceratopogonidae larvae	0.19	0.85	1.16
Detritus	-----	0.85	1.16
Oligochaeta	0.19	0.34	1.16

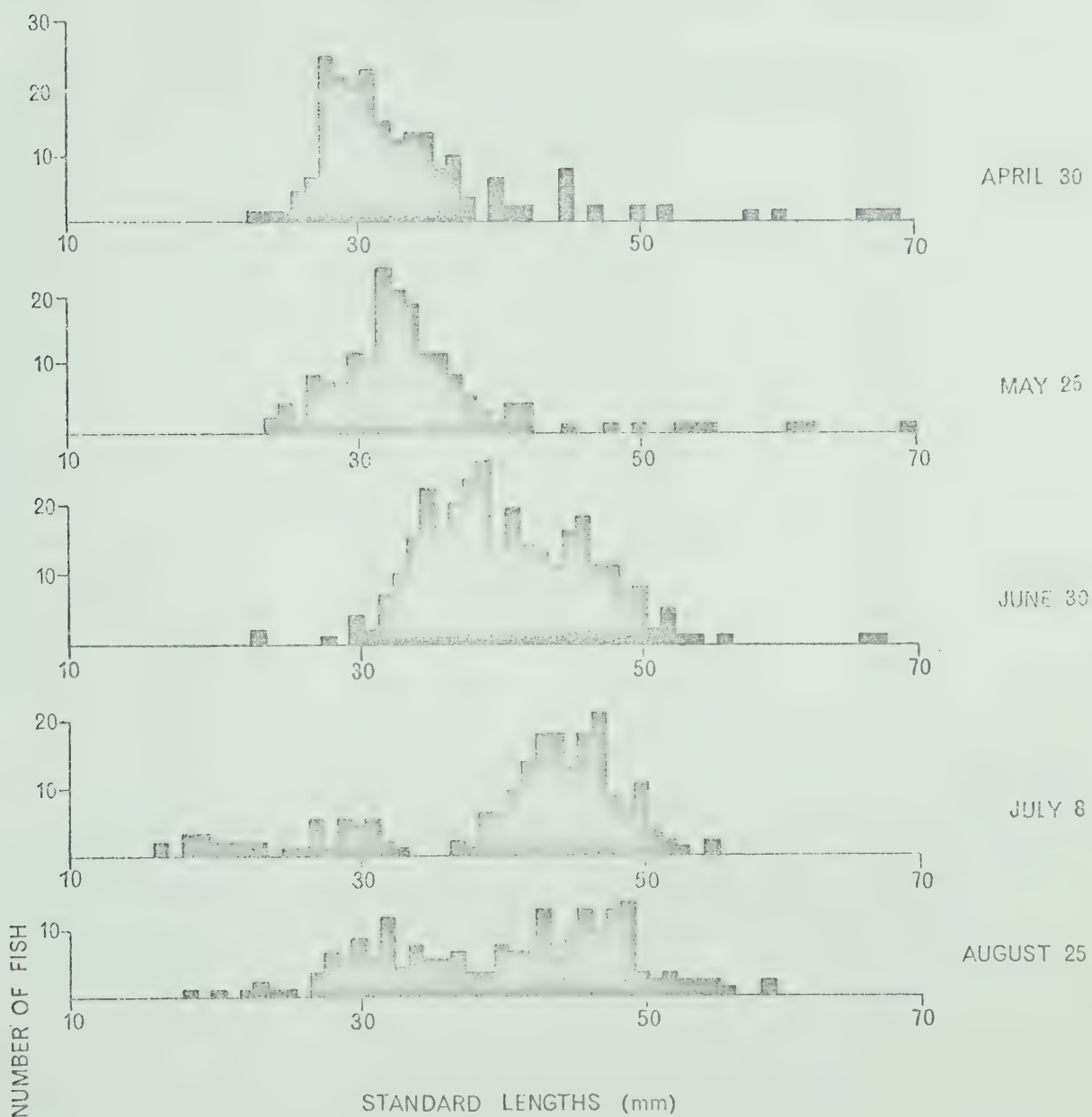
Appendix B. Summary of data on spine types.

	Random Samples N=800	Residence Point Males N=160	Fish parasitized by <u>S. solidus</u> N=66
Males	41.9%	-----	28.8%
Females	50.9%	-----	57.6%
4 Dorsals	0.03%	0.0%	0.0%
5 Dorsals	61.4%	63.1%	57.6%
6 Dorsals	38.4%	36.9%	42.4%
2 Pelvics	58.5%	59.4%	56.1%
1 Pelvic	3.3%	4.4%	0.0%
0 Pelvics	32.3%	27.5%	33.3%
Girdle remnants	6.0%	8.8%	10.6%

The ratios of spine types in males do not differ significantly from those in random samples (Chi-square= 3.57 at 6 df.)* The ratios of spine types in parasitized fish do not differ significantly from those in random samples (Chi-square=4.83 at 6 df.) However, the sex ratio is different for parasitized fish. Statistically, the difference is not significant at the 5% level (Chi-square=10.13 at 8 df), but there may be some biological significance (ie. a difference in susceptibility to infection).

* Chi-squares were calculated using a 2 X r contingency table.

Appendix C. Standard length frequencies from random samples taken at Residence Point in 1970.



Appendix D. Data for unidentified parasites.

Two unidentified parasites were quite common. Parasite 'W' existed in the form of small white spots (probably encysted metacercaria) on the skin of the fish. Parasite 'Wa' was probably a microsporidean, which formed large cysts in the muscle tissue of the fish. The following table shows the extent of parasitism by these two organisms during the summer of 1970:

Date	Percentage of fish infected		Sample Size
	'W'	'Wa'	
April 30	12%	0%	50
May 8	11	1	100
May 14	2	0	100
May 22	16	0	50
May 26	11	1	100
June 2	0	0	100
June 9	2	0	50
June 16	0	3	100
June 23	0	3	100
June 30	34	6	50
July 7	1	6	100
July 14	0	3.4	89
July 21	12	2	50
July 28	1	2	100
August 4	0	1	50
August 11	8	2	100
August 18	0	0	100
August 25	0	0	100
September 1	10	0	50
October 17	6	0	50

Of the fish infected by 'W', 68% had two pelvic spines, 24% had none, and 8% had pelvic girdle remnants. 56% were males. Of the fish infected by 'Wa', 64% had two pelvic spines, 24% had none, 8% had one, and 4% had pelvic girdle remnants. 60% of these fish were males. Statistically, these ratios do not differ significantly from those of random samples.

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